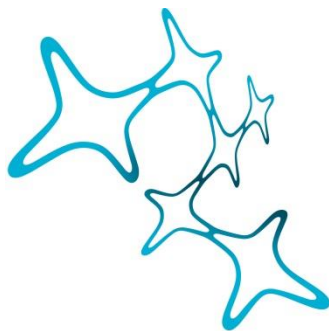

NEUROGAME: NEURAL MECHANISMS UNDERLYING COGNITIVE IMPROVEMENT IN VIDEO GAMERS

Yannik Hilla



Graduate School of
Systemic Neurosciences

LMU Munich



Dissertation at the
Graduate School of Systemic Neurosciences
Ludwig-Maximilians-Universität München

17th January 2023

Supervisor

Prof Dr Paul Sauseng

Department of Psychology/Research Unit Biological Psychology

Ludwig-Maximilians-Universität München

First Reviewer: Prof Dr Paul Sauseng

Second Reviewer: Dr Heinrich René Liesefeld

Date of Submission: 17th January 2023

Date of Defense : 23rd May 2023

Abstract

The video game market represents an influential and profitable industry. But concerns have been raised how video games impact on the human mind. There are reservations that video gaming may be addictive and foster aggressive behaviour. In contrast, a convincing body of research indicates that playing video games may improve cognitive processing. The exact mechanism thereof is not entirely understood. Most research suggests that video games train individuals in learning how to employ attentional control to focus on processing relevant information, while being able to suppress irrelevant information. Thus, video game players acquire the ability of being able to develop strategies to process information more efficiently. However, no algorithmic solution therefore has been provided yet. Thus, it is not clear which and how attentional control functions contribute to these effects. Moreover, neural mechanisms thereof are not well understood. We hypothesized that alterations in alpha power, i.e., modulations in brain oscillatory activity around 10 Hz, represent a promising neural substrate of video gaming effects. This was because, alpha activity represents an established neural correlate of attention processing given that its amplitude modulation corresponds to alterations in information processing. We investigated this by relating differential cognitive processing in video game players to changes in alpha power modulation. Moreover, we tried to imitate this effect using non-invasive brain stimulation. We were successful in achieving the former but not the latter. We provide a reasonable explanation for this. Thus, our results mostly support our hypothesis according to which altered alpha power may account for gaming effects.

Keywords: transfer effects, computational modeling, attentional control, brain stimulation

Contents

General Introduction	4
Adverse and Beneficial Effects of Video Gaming on the Human Mind	4
Adverse Effects: Aggression and Addiction	4
Beneficial Effects: Cognitive Improvements	6
Aims and Scope of this Thesis	12
Does Alpha Power Modulation Indeed Operationalize Attentional Control? .	12
Do Video Gaming Effects Correlate with Task-Specific Alpha Amplitude Modulation?	13
Is it Possible to Imitate Video Gaming Effects by Means of Non-Invasive Brain Stimulation?	14
Research Projects	16
Cause or Consequence? Alpha Oscillations in Visuospatial Attention	16
Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation	26
Alpha-tACS Alters Attentional Control but not Cognitive Functions as Video Games Do	43
General Discussion	71
A Computational Model of Attentional Control Based on the Theory of Visual Attention (TVA) to Operationalize Video Gaming Effects	72
Improved TVA Information Processing Capacity in Video Game Players Relates to Higher-Level Selective Attention Processing	72
Extending the TVA Computational Model by a Saliency Map Framework to Allow for Flexibility Despite Fixed Cognitive Capacities	75
Alpha Oscillatory Activity as Neural Substrate of TVA Information Processing	77
Summary	80

NEUROGAME	3
Feasibility of the Extended TVA Model to Explain Video Gaming Effects . . .	81
Future Research	83
Conclusion	85
References (General Introduction and Discussion)	86
Acknowledgments	99
Curriculum Vitae	100
List of Publications	102
Eidesstattliche Versicherung/Affidavit	104
Declaration of Author Contributions	105
Cause or Consequence? Alpha Oscillations in Visuospatial Attention	105
Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation	106
Alpha-tACS Alters Attentional Control but not Cognitive Functions as Video Games Do	107

General Introduction

According to a survey conducted by the Entertainment Software Association (2022)¹, approximately 66 % of the American population played video games for at least one hour (and on average 13 hours) per week in 2021. Therefore, they used a tablet, PC, gaming consoles, their smartphone or more than one of these devices. Hereby, puzzle, arcade, action (role-play/ adventure), shooter and strategy video games were among the more and racing, driving, fighting and sports video games among the lesser prevalently played video games. Respondents stated that their reasons for playing video games were that it was fun, inspiring, mentally stimulating, and stress relieving. Moreover, video gaming appeared to have contributed to building and strengthening relational bonds with family members and peers. Besides that, approximately 43.4, 56.1 and 60.4 billion dollars of profit have been made by means of video game sales and sales of related products, e.g., consoles, in 2019, 2020 and 2021, respectively (Entertainment Software Association, 2022). Thus, the video game market represents an extremely influential and increasingly profitable industry.

Adverse and Beneficial Effects of Video Gaming on the Human Mind

Adverse Effects: Aggression and Addiction. In this regard, concerns have been raised as to how video games impact on the human mind. One of them refers to the reservation that playing video games, in particular shooter video games, might foster aggressive behavior given that video game players may experience and conduct extreme violence during playing, e.g. killing opponents with weapons. Some politicians and journalists even went so far as to claim that perpetrators might have been motivated to commit rampages by video games (see, e.g., Dittmayer (2014), for an overview on this discussion in Germany). In fact, the scientific literature on the association between playing video games, aggression, and crime is quite inconclusive. On the one hand, there are indications that playing video games might indeed slightly increase aggressive behavior (Furuya-Kanamori &

¹ Estimates and predictions were made based on survey reports of approximately 4000 American respondents.

Doi, 2016; Greitemeyer, 2022). On the other hand, playing video games also appears to be associated with stress release, and thus maybe reduced aggression (Cunningham, Engelstätter, & Ward, 2016; Markey, Markey, & French, 2015). This inconsistency is likely related to diverging experimental designs and sample characteristics, e.g., methods having been applied to analyze data, players' motivations to play video games, their personality traits, sociodemographic influences, the actual game play of the video games having been played, etc. (Bonus, Peebles, & Riddle, 2015; Ferguson, Copenhaver, & Markey, 2020; Ferguson, Olson, Kutner, & Warner, 2014; Kersten & Greitemeyer, 2022; Lee, Kim, & Choi, 2021). Besides that, one should bear in mind that both popular opinions and empirical results may be biased by prejudices and stereotypes. Markey, Ivory, Slotter, Oliver, and Maglalang (2020), for instance, found that playing video games was considered a more likely cause for committing rampage in white perpetrators as compared to black ones. This implies that racial stereotypes might bias individuals' perception of the influence of video games. Thus, playing some video games might indeed impact on aggression in the short run. But, it is unlikely to significantly contribute to individuals actually conducting violent behavior.

Another concern is that playing video games may be highly addictive. In fact, the *World Health Organization* recently included *gaming disorder* in its 11th revision of the *International Classification of Diseases* (ICD-11) (World Health Organisation, 2019/2020). Thus,

gaming disorder is characterised by a pattern of persistent or recurrent gaming behaviour ('digital gaming' or 'video gaming'), which may be online (i.e., over the internet) or off-line, manifested by: 1. impaired control over gaming (e.g., onset, frequency, intensity, duration, termination, context); 2. increasing priority given to gaming to the extent that gaming takes precedence over other life interests and daily activities; and 3. continuation or escalation of gaming despite the occurrence of negative consequences (World Health Organisation, 2019/2020).

Aarseth and colleagues (2017), however, criticized this conceptualization by pointing out

that it lacked specificity. On top of that, they raised concerns if pathologizing video gaming fostered stigmatization. In fact, the ICD-11 description of gaming disorder appears to coincide with the common stereotype of video game players being perceived as couch potatoes neglecting their hygiene and social lives for the sake of their video game characters. Furthermore, the prevalence of video gaming disorder varies remarkably depending on sample characteristics, such as nationality, age and gender, and methods having been applied to analyze data (e.g., between 0.7 and 27.5 %) (Kim et al., 2022; Mihara & Higuchi, 2017; Stevens, Dorstyn, Delfabbro, & King, 2021). Thus, data on gaming disorder is likely confounded by social desirability and stereotypes about video game players. In support of this, a study on stigmatization of Chinese *eSports* athletes, i.e., individuals playing video games for competitive/professional reasons, showed that

eSports players have experienced two specific types of stigma over the past twenty years. First, adults simply associate *eSports* with gaming addiction that has led young people to miss out on higher education potentially leading to good careers. Second, these youth may be perceived, somewhat naively, as celebrating their gaming addiction by engaging in *eSports* as a professional pursuit to cover up the fact that they are losers, causing them to lose mianzi ('face') (Zhao & Zhu, 2021).

Thus, there are indications that video game players may develop an obsessive desire to play video games. To evaluate, treat and investigate such behavior, however, a more unbiased consensus on which characteristics of video gaming are to be considered as pathological will be required.

Beneficial Effects: Cognitive Improvements. Besides that, there is a convincing and growing body of research indicating that video gaming was associated with cognitive improvement. For instance, video game players have been shown to outperform control individuals in psychometric tasks operationalizing cognitive functions, such as perception (R. Li, Polat, Scalzo, & Bavelier, 2010), memory (Blacker & Curby, 2013), executive control

(Cain, Landau, & Shimamura, 2012), attention (Green & Bavelier, 2003) and probabilistic inference (Schenk, Lech, & Suchan, 2017). Likewise, individuals with hardly any or without video gaming experience displayed similarly enhanced cognitive processing after having participated in a video game training (Bejjanki et al., 2014; Blacker, Curby, Klobusicky, & Chein, 2014; Green & Bavelier, 2003; Green, Pouget, & Bavelier, 2010; Strobach, Frensch, & Schubert, 2012). Furthermore, playing video games seems to elicit improvements in skills beyond the scope of psychometric tasks, e.g., flight (simulation) performance and surgical proficiency (Chiappe, Conger, Liao, Caldwell, & Vu, 2013; Gopher, Well, & Bareket, 1994; Lu et al., 2022; Lynch, Aughwane, & Hammond, 2010; Schlickum, Hedman, Enochsson, Kjellin, & Felländer-Tsai, 2009). Moreover, video games have been successfully applied to augment clinical treatment of cognitive impairment, e.g., symptoms associated with amblyopia (Foss, 2017; Gambacorta et al., 2018; R. W. Li, Ngo, Nguyen, & Levi, 2011) and attention deficit hyperactivity disorder (Kollins et al., 2020), and to compensate for age-related cognitive decline (Anguera et al., 2013). Interestingly, such effects had been more prevalently observed in individuals after they had played action and multi-player online battle arena video games or games with similar characteristics (Achtman, Green, & Bavelier, 2008; Bediou et al., 2018b; Large et al., 2019). Thus, these of all video games notorious for fostering aggressive behavior (see above) might in fact improve cognitive processing.

The exact mechanism of these *transfer effects*, i.e., alterations in cognitive processing coinciding with an improvement in video game performance even though playing video games does not directly train them, is not yet fully understood. Bavelier, Green, Pouget, and Schrater (2012), for instance, proposed that video game players' superior performance in cognitive processing could be explained by video gaming inadvertently training a cognitive function which several cognitive processes have in common. Hereby, they argued for probabilistic inference as a prime candidate (Bavelier, Green, et al., 2012; Green & Bavelier, 2012). Probabilistic inference refers to the ability of learning to anticipate events from statistical regularities and develop behavioral strategies accordingly. Statistical regularities,

in turn, represent the foundation of video game play characteristics. Thus, video game players might passively practice to recognize statistical regularities of video games and to develop and conduct strategies to succeed during gaming. Hereby, operand conditioning likely represents a vital learning mechanism given that a failure to correctly anticipate an event, e.g., an opponent, will require them to adjust their behavior by the point of success (Koepp et al., 1998; Kühn et al., 2011; Schenk et al., 2017). As a result, video game players' probabilistic inference may improve, and cognitive functions relying on probabilistic computations might be altered, e.g., perception (Deroy, Spence, & Noppeney, 2016). In support of this, it has been shown that video game players displayed superior probabilistic inference in several tasks (Green et al., 2010; Schenk et al., 2017). Moreover, individuals developed enhanced probabilistic inference as a result of playing action video games (Green et al., 2010). Besides that, Bejjanki and colleagues (2014) found that such learning effects coincided with video game players displaying an improving signal-to-noise ratio. Thus, the conjunction between probabilistic inference and attentional control functions seems to represent a crucial mechanism in transfer effects associated with video gaming (Bavelier & Green, 2019; Green & Bavelier, 2012). In this regard, attentional control refers to a set of attention and executive functions to enhance processing relevant information, while being able to suppress irrelevant information (Bavelier & Green, 2019). Thus, video game players appear to learn to recognize statistical regularities and to come up with successful strategies rather *efficiently* than *passively* given that attentional control functions are trained and deployed to facilitate these learning processes. In support of this, a meta-analysis showed that video game players most reliably outperform control individuals in tasks operationalizing attentional control (Bediou et al., 2018b, 2018a). Moreover, these effects coincided with alterations in neural processing. Bavelier and colleagues (2012) and Föcker and colleagues (2018), for instance, found that video game players' superior performance in two discrimination tasks was associated with them consulting the fronto-parietal top-down network relevant for operating attentional control functions less strongly than control

individuals (Corbetta, Patel, & Shulman, 2008). In line with the *neural efficiency* theory (Haier et al., 1988), these results indicate that video game players had to put less effort into executing the paradigm and hence displayed a weaker brain activity. Moreover, Tanaka and colleagues (2013) showed that inter-individual performance differences in a match-to-sample task between video game players and control individuals were correlated with volumetric dissimilarities in the fronto-parietal top-down network. Furthermore, video game players' superior visuospatial attention processing coincided with enlarged posterior P2 and P3 event-related potentials (Wu et al., 2012). On top of that, their ability to identify targets and ignore distractors in rapid streams of visual stimuli was associated with stronger modulations of steady-state visually evoked potentials (SSVEPs) and the anterior N1 (Föcker, Mortazavi, Khoe, Hillyard, & Bavelier, 2019; Mishra, Zinni, Bavelier, & Hillyard, 2011). Thus, playing video games might alter video game players' neural networks in accordance to them learning to recognize statistical regularities and to apply attentional control functions to develop efficient behavioral and cognitive strategies resulting in overall enhanced cognitive processing. Therefore, this hypothesis is also referred to as *learning to learn* hypothesis (Bavelier & Green, 2019; Bavelier, Green, et al., 2012) (see, Figure 1, for a schematic visualization).

Hilgard, Sala, Boot, and Simons (2019), however, pointed out that effect size estimations reported by Bediou and colleagues (2018b) might have been confounded by publication bias. In detail, they criticized that effects might have been driven by the publication outcome of foremost one particular research group, and over-estimated given that some of the effect sizes included in the analysis may have been considered as original even though these had been likely based on the same sample of participants. Besides that, video game training effects may be unreliable. Boot, Kramer, Simons, Fabiani, and Gratton (2008), for instance, were only partially able to replicate cognitive improvements by means of video game training. Moreover, while Schubert and colleagues (2015) were able to demonstrate enhanced temporal sensitivity and speed of information processing in video game players, they could not elicit the same effects in non-video game players using a video game training.

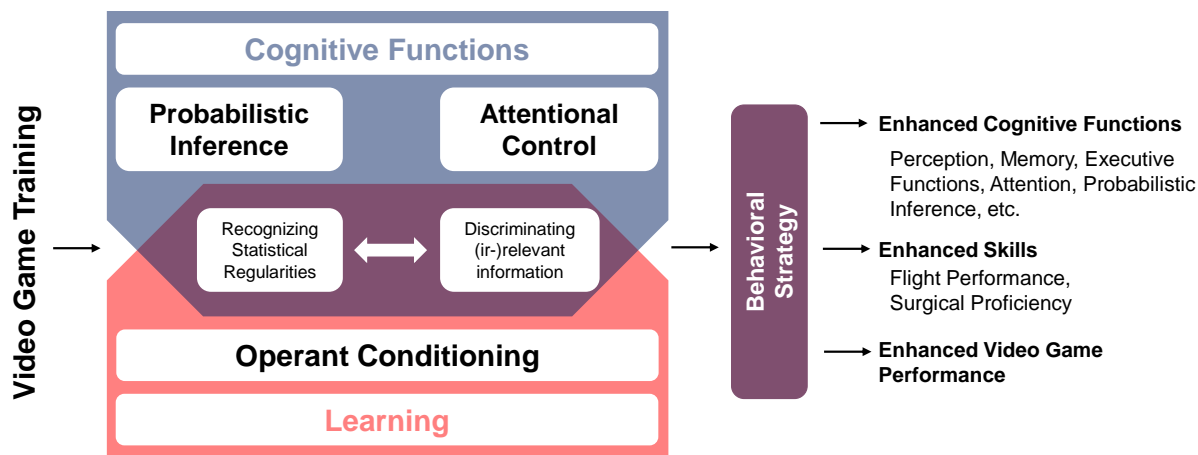


Figure 1. Schematic Visualization of the *Learning to Learn Hypothesis*. Game play characteristics of video games are based on statistical regularities. Video game players learn to anticipate these regularities in the course of playing video games (i.e., *probabilistic inference*). *Operant conditioning* represents a fundamental learning mechanism in this regard as video game players learn to adapt their strategies through success and failure. Therefore, *attentional control* functions to enhance relevant and to suppress irrelevant information processing come into force. Thus, video game players learn to deploy cognitive resources efficiently by learning to optimize the signal-to-noise ratio. As a result, video game players acquire the ability to develop successful *behavioral strategies* as reflected by superior performance in psychometric tasks (*enhanced cognitive processing*), everyday complex tasks (*enhanced skills*) and *enhanced video game play performance*.

Furthermore, it is still inconclusive which and how attentional control functions contribute to video gaming effects. This is because, empirical findings on the association between attentional control and video gaming had been ambiguous and/or inconsistent. For instance, Bavelier and colleagues (2012) and Föcker and colleagues (2018) suggested that a lack of neural modulation in the fronto-parietal top-down network might be an indication for efficient attentional deployment in video game players given that this effect was associated with superior performance in a task requiring attentional control functions. In contrast, this effect could also indicate that video game players might have used a strategy independent of attentional control which just coincided with a better performance given that there was actually no indication for a recruitment of this network despite attentional deployment. A similar logic applies to the effect reported by Mishra and colleagues (2011) according to which a weaker modulation of SSVEPs in response to unattended stimuli was suggested to reflect enhanced top-down inhibition in video game players. However, SSVEPs usually correlate with the extent of attentional deployment towards stimuli (Vialatte, Maurice, Dauwels, & Cichocki, 2010). Therefore, it seems more likely that this effect reflected a lack of deployment of attentional resources rather than an active suppression. Furthermore, this effect may be somehow controversial in any case provided that Krishnan, Kang, Sperling, and Srinivasan (2013) found the opposite effect when they compared SSVEPs between action and real-time strategy video game players having performed a very similar task as applied by Mishra and colleagues (2011). On top of that, there are also indications that video gaming transfer effects might be completely independent of attentional control. Both Schubert and colleagues (2015) and Wilms and colleagues (2013), for instance, found that video game players displayed superior temporal sensitivity and processing speed in comparison to non-video game players. However, they could not show that video game players exhibited improved top-down control or visuospatial attention in addition to that.

Thus, there is remarkable evidence that playing video games might elicit cognitive improvements by training individuals in applying probabilistic inference in conjunction with

attentional control functions to develop efficient behavioral and cognitive strategies. However, further research will be required to investigate which and how these cognitive functions relate to transfer effects associated with video gaming.

Aims and Scope of this Thesis

A particularly suitable neural mechanism therefore may be alpha activity, i.e., modulations in brain oscillatory activity around 10 Hz. This is because, alpha activity is widely considered as a neural substrate of attentional control given that its attenuation (*desynchronization*) has been frequently observed to go along with facilitated information processing, while its increase (*synchronization*) coincided with the opposite effect (Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Jensen & Mazaheri, 2010; Klimesch, 2012; Klimesch, Fellinger, & Freunberger, 2011, 2011; Klimesch, Sauseng, & Hanslmayr, 2007; Peylo, Hilla, & Sauseng, 2021). In this regard, alpha power is particularly known for its retinotopic modulation in association with the focus of attention. Thus, alpha activity typically desynchronizes stronger in hemispheres contralateral to the focus of attention, while it sometimes also increases in ipsilateral hemispheres (Capotosto, Babiloni, Romani, & Corbetta, 2009; Jensen & Mazaheri, 2010; Rihs, Michel, & Thut, 2009; Sauseng et al., 2009; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). Furthermore, the opposite effect has been observed in response to distracting stimuli in the visual field (Sauseng et al., 2009; Worden, Foxe, Wang, & Simpson, 2000). Therefore, alpha power modulation appears to contribute to enhancing relevant information processing and to suppressing irrelevant information processing, which correlates with the functional properties of attentional control functions as described in the *learning to learn* hypothesis (Bavelier & Green, 2019; Bavelier, Green, et al., 2012). Thus, we propose that altered alpha power modulation may account for transfer effects related to video gaming.

Does Alpha Power Modulation Indeed Operationalize Attentional Control?

However, recently, these functional properties of alpha power modulation have been

challenged. Noonan and colleagues (2016), for instance, questioned whether alpha synchronization was indeed related to information inhibition given that they had not been able to relate distractor cueing effects with increased alpha power. Individuals participating in their studies performed modified Posner's cueing tasks where both target and distractor locations had been cued. The authors hypothesized that participants would make use of these cues to enhance target and to suppress distractor processing as reflected by reduced reaction times towards target stimuli. Their behavioral results were in line with these hypotheses. However, while individuals displayed on average a decreased alpha power in response to target stimuli, they did not show an increased activity in response to distractors in the respective contralateral hemispheres. Thus, the distractor cueing effect did not correlate with the anticipated alpha power modulation. Moreover, Antonov, Chakravarthi, and Andersen (2020) argued that alpha power modulation might in fact represent an epiphenomenon of attentional orienting rather than a functional mechanism thereof. In support of this, they found that individuals displayed a modulation earlier in SSVEPs than in alpha power prior to target detection in rapid streams of visual stimuli. Furthermore, again individuals did not display alpha synchronization in response to distractor stimuli. Thus, Antonov and colleagues (2020) concluded that alpha power unlikely represented a causal mechanism in visuospatial attention given that it had not been the first neural response being modulated in anticipation of target stimuli, and in addition to that, not having been modulated by distractor stimuli. We addressed these concerns in a recently published opinion article and provided arguments in favor of alpha power representing a neural substrate of visuospatial attention nevertheless (Peylo et al., 2021) (see, **Cause or Consequence? Alpha Oscillations in Visuospatial Attention in Research Projects**, for more details).

Do Video Gaming Effects Correlate with Task-Specific Alpha Amplitude Modulation? Besides that, we were not the first to suspect that alpha power modulation might reflect a neural mechanism of cognitive alterations related to video gaming, and to investigate this association. Mathewson and colleagues (2012), for instance, found an

association between individuals' improved shifting abilities and their frontal alpha power recorded at the onset of study participation after training them in the *Space Fortress* video game. Furthermore, Hazarika, Kant, Dasgupta, and Laskar (2018) and Hazarika and Dasgupta (2020) found that inter-individual differences in alpha power coincided with differential attention processing performance between video game players and control individuals. However, these studies did not investigate task-related alpha power modulations, e.g., related to stimulus processing. Thus, it is difficult to conclude whether alpha power modulations indeed accounted for differential cognitive processing in video game players. We addressed this issue in a recently published study (Hilla, Von Mankowski, Föcker, & Sauseng, 2020). Thus, we showed that video game players' speed of information processing improved in the course of time on task and that this effect, in turn, correlated with an increase in alpha amplitude attenuation (see, **Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation in Research Projects**, for more details).

Is it Possible to Imitate Video Gaming Effects by Means of Non-Invasive Brain Stimulation? However, this was just a correlational relationship. Thus, our EEG study results did not provide sufficient evidence in favor of altered alpha power modulation accounting for differential cognitive processing in video game players. Furthermore, our approach did only allow to operationalize individuals' speed of information processing but not their attention control functions, e.g., top-down control and visuospatial attention processing. However, in order to provide strong evidence that alpha power indeed operationalized attentional control and thus accounted for differential cognitive processing in video game players, a relationship between altered alpha power, top-down/visuospatial attention processing and speed of information processing needed to be established. We addressed these issues by conducting a non-invasive brain stimulation study (Hilla, Link, & Sauseng, 2023). The aim of this study was to demonstrate that transcranial alternating current stimulation (tACS), an established method to modulate brain oscillatory activity

(Helfrich et al., 2014; Kemmerer et al., 2022), applied at alpha frequency (i.e., ca. 10 Hz) over individuals' posterior parietal cortex could alter their speed of information processing and top-down/visuospatial attention processing. Thus, we would have been able to imitate our previous video gaming effect and to establish that this effect was related to alpha power modulation impacting on attentional control (see, **Alpha-tACS Alters Attentional Control but not Cognitive Functions as Video Games Do in Research Projects**, for more details).

Research Projects

Cause or Consequence? Alpha Oscillations in Visuospatial Attention

- Peylo, C., **Hilla**, Y., & Sauseng, P. (2021). Cause or consequence? Alpha oscillations in visuospatial attention. *Trends in Neurosciences*, 44(9), 705-713.
- C.P.: Conceptualization, Writing - Review & Editing. **Y.H.**: Conceptualization, Writing - Review & Editing. P.S.: Conceptualization, Writing - Review & Editing, Funding Acquisition, Resources, Validation.
- Charline Peylo and I contributed equally to conceptualizing, writing, reviewing and editing the article (shared first-authorship).

Opinion

Cause or consequence? Alpha oscillations in visuospatial attention

Charline Peylo,^{1,2} Yannik Hilla,^{1,2} and Paul Sauseng^{1,*}

A well-established finding in the literature of human studies is that alpha activity (rhythmical brain activity around 10 Hz) shows retinotopic amplitude modulation during shifts in visual attention. Thus, it has long been argued that alpha amplitude modulation might play a crucial role in attention-driven alterations in visual information processing. Recently, there has been a revival of the topic, driven in part by new studies directly investigating the possible causal relationship between alpha activity and responses to visual input, both neuronally and perceptually. Here, we discuss evidence for and against a causal role of alpha activity in visual attentional processing. We conclude with hypotheses regarding the mechanisms by which top-down-modulated alpha activity in the parietal cortex might select visual information for attentive processing.

Alpha amplitude modulation during shifts in visuospatial attention

The participant is wired up, a full set of electroencephalogram (EEG) electrodes attached to the scalp. The room is dimly lit, and the participant fixates a crosshair in the center of the screen in front of them. They are instructed to covertly shift their visual attention (i.e., without moving their gaze from the fixation cross) either to the left or to the right, depending on a spatial cue they receive. The EEG is recorded. The participant shifts their attention to the left. What can be observed now, even with the naked eye, is that rhythmical brain activity around 10 Hz, so called alpha waves, is suppressed at right parietal electrode sites while it might increase in amplitude over the left parietal cortex (Figure 1).

Such attention-related modulation of posterior EEG alpha amplitude is considered a particularly consistent cognition-induced EEG oscillation pattern and it has frequently been reported [1–4]. In this context, decreased alpha amplitudes were discussed as neural substrate of cortical activation [5–8] related to facilitated information processing [9], while increased alpha amplitudes have been considered a marker of cortical deactivation associated with inhibitory processes of cognition [10–12]. The argument can be made that if, as described above, alpha waves are suppressed contralateral (and potentially increased ipsilateral) to the cued visual hemifield, posterior alpha amplitude modulation may be a neural substrate of focused, directed attention. However, this interpretation has been the matter of recent debate questioning whether modulations of EEG **alpha activity** (see [Glossary](#)) represent a causal mechanism of cortical activation/deactivation in visuospatial attention or whether they are merely an epiphenomenal consequence of shifted visuospatial attention.

Alpha activity is a prominent rhythmic brain activity in humans (particularly during rest). It has been considered an effective marker of cortical excitability [10,13–15]. In the context of visuospatial attention, as mentioned, modulations of alpha activity reflect shifts of visuospatial attention in a retinotopic manner, with suppressed alpha waves at loci of attention [3,16,17] and increased alpha at brain areas processing unattended information [1,2,4]. This retinotopically organized

Highlights

Modulations of electroencephalogram alpha amplitude have long been associated with visuospatial attention, but whether alpha power changes are causally involved in attention shifts or reflect a consequence of them is a matter of ongoing debate.

We evaluate recent findings providing evidence for both of these two perspectives.

We discuss the extent to which the temporal dynamics of alpha activity and extrinsic modulation of alpha amplitude can be used as a basis for arguing for or against alpha activity as a causal substrate of visuospatial attention.

We also discuss whether alpha activity implements attention by gain control in the early visual cortex.

A potential mechanism by which alpha activity in higher visual areas implements attentional gating is introduced.

¹Department of Psychology, Ludwig-Maximilians-Universität München, Munich, Germany

²Contributed equally

*Correspondence: paul.sauseng@imu.de (P. Sauseng).



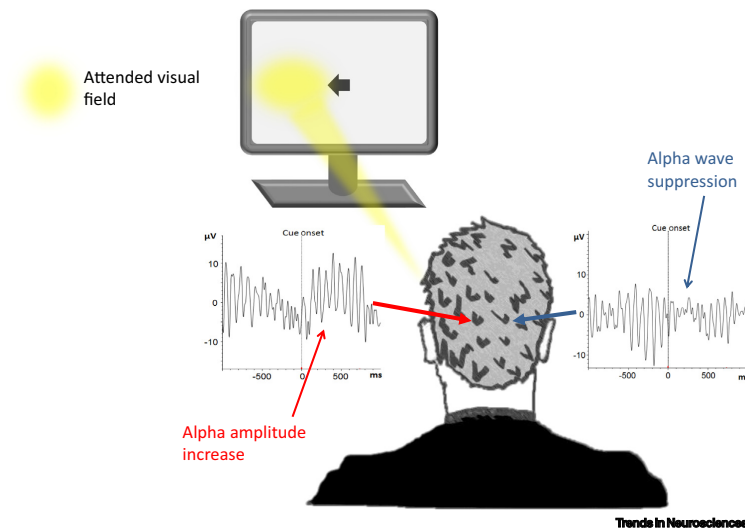


Figure 1. Retinotopic modulation of posterior alpha amplitude during covert shifts of visual attention. A participant is instructed to fixate the middle of a screen. When a cue appears (arrow pointing to the left), visual attention has to be shifted into the respective visual hemifield (i.e., the left hemifield) without any gaze movement. This shifting of visuospatial attention is usually associated with the suppression of alpha waves at parietal electroencephalogram (EEG) recording sites contralateral to the attended hemifield (in this example, the right hemisphere) and is often paralleled by an alpha amplitude increase ipsilateral to the cued hemifield (here, the left).

alpha activity in early visual areas, however, seems to be under top-down control by frontoparietal networks [3, 18–20]. Modulation of EEG alpha activity in the visual cortex could then reflect top-down-controlled changes in local excitability that may in turn affect the processing of incoming visual stimuli (**gain control**). Recent studies have led to a resurgence of interest in alpha activity's role in visual attention. There has been doubt about whether alpha activity plays a causal role in attentional processing by implementing gain control in early visual areas [21–23] or even that alpha activity is causally involved in visuospatial attention at all [24]. Here, we evaluate several arguments for as well as against a causal role of alpha activity in visuospatial attention, and more specifically whether modulation of alpha activity reflects gain control in early visual areas.

Temporal dynamics of visuospatial attention and alpha activity: arguments against a causal role?

If alpha amplitude modulation is causally involved in attention-related gain control of incoming signals, a clear prediction ensues: alpha amplitude should be the first measurement capturing any attentional effects [i.e., there should be attention-related alpha amplitude changes prior to any effects on event-related potentials (ERPs) or response times]. In line with this prediction, compared with early target-evoked ERPs [25, 26], alpha activity seems to exhibit effects much earlier [2–4]; namely, already in response to an attentional cue. However, as correctly pointed out in the context of a recent study [24], this does not necessarily lend evidence to the idea that alpha activity represents the initial neural response of visuospatial attention shifts. To examine the issue further, the aforementioned study measured **steady-state visually evoked potentials (SSVEPs)** as a proxy for neural activity from the early visual cortex modulated by visual attention [24]. Additionally, EEG alpha activity and behavioral attention parameters were acquired. The

Glossary

Alpha activity: neural oscillatory activity in a frequency range around 10 Hz in humans. It has been claimed that the amplitude of alpha activity is associated with cortical excitability.

Duty cycle: the excitatory part of a neural oscillation's cycle. Usually the duty cycle is characterized by increased neuronal firing.

Entrainment: alignment of intrinsic oscillatory brain activity using stimulation approaches, usually rhythmic ones, such as sensory, electrical, magnetic, or ultrasonic stimulation. This might lead to increased amplitude at respective and/or related frequency ranges or it could result in alignment of the neural oscillation's instantaneous phase.

Gain control: adjustment of neural activity to put greater or lesser weight on the processing of a specific incoming stimulus. Gain control has been discussed, for instance, to reflect a physiological correlate of a spotlight of attention in the early visual cortex [61].

Gating: a neural mechanism to modulate the flow of low-level information to higher visual cortical areas.

Noninvasive brain stimulation (NIBS): noninvasive techniques to modulate brain activity. Examples of NIBS techniques are TMS and tES. TMS alters neuronal activity by means of electromagnetic pulses generated by a coil that is held against the participant's scalp. tES stimulates neuronal tissue by means of electric currents applied via electrodes attached to the scalp. To gear into ongoing oscillatory brain activity, a series of electromagnetic pulses (rTMS) or rhythmical fluctuations of electrical current (tACS) can be delivered.

Phase coherence: a measure of the presence and strength of a systematic relationship between the phase of two distinct neural oscillations (e.g., at different brain sites, with different frequencies). Phase coherence is high if the phase relationship is consistent over time (usually across trials) and low if the phase relationship varies randomly.

Posner task: experimental paradigm to investigate the shifting of visuospatial attention. Participants are asked to keep their gaze at a fixation cross in the middle of a screen. Then, the left or the right visual hemifield is cued. Participants are asked to covertly shift their visual attention into the cued hemifield

Trends in Neurosciences



authors observed an attention-related increase of SSVEP amplitudes shortly prior to lateralized suppression of alpha waves. Modulation of alpha activation was clearly lagging behavioral estimates of when attention was shifted to the periphery. Therefore, it was concluded that alpha amplitude modulation cannot be the causal substrate of visuospatial attention but rather must be the consequence of shifted attention.

However, in a similar study [23] lateralized alpha modulation preceded attentional alterations of SSVEPs in earlier visual areas. Nevertheless, alpha activity did not have any direct impact on SSVEPs in the visual cortex. Thus, if alpha activity played a direct role in visuospatial attentional shifting, most likely it would not do so by altering sensory gain control in visual areas (as discussed later in greater detail). This is supported by recent findings, which also suggest independence between posterior alpha activity and SSVEPs [22].

Consequently, one could conclude that modulation of alpha activity is not causally involved in shifts of visual attention – but not so fast! First, whereas SSVEPs have a notable signal-to-noise-ratio due to averaging over trials, alpha activity can be far noisier. All signals that do not constitute the evoked response should, in theory, be eliminated from the SSVEP due to averaging. Alpha amplitude is usually rectified before averaging over trials, and therefore random noise overlapping in frequency space with alpha activity will be picked up by the signal. Thus, a high level of noise could make it impossible to relate alpha amplitude with SSVEPs. Second, to obtain estimates of alpha amplitude it is necessary to filter raw EEG data in one way or another. All filters will lead to smearing in the temporal and spectral domains. The exact temporal evolution of true alpha activity, therefore, is difficult to determine. Third, shifting visual attention does not solely modulate alpha amplitude. A concurrent increase in theta activity (rhythmic activity at frequencies slightly lower than the alpha frequency band) has been reported (e.g., [3,27]). Due to spectral smearing when filtering EEG data, this transient increase in theta activity could 'leak' into the alpha band and make the latter look as if its amplitude were decreasing far later than it is the case for the actual, underlying alpha activity.

Most importantly, however, as pointed out in the discussion later, modulation of alpha activity could be causally involved in the implementation of visual attention even if it lags behind other effects in early visual cortex (e.g., SSVEPs); namely, if higher visual areas used alpha activity for filtering or **gating** of upstream visual information.

We would argue then that, based on the findings discussed earlier, it would be premature to dismiss a causal relation between alpha amplitude modulation and shifts of visual attention. To recapitulate: (i) the exact temporal evolution of alpha amplitude modulation is difficult to determine; (ii) genuine alpha activity can be distorted by spectral smearing due to filtering data; and (iii) alpha activity could be used as an attentional implementation mechanism further up the cortical hierarchy.

Closed-loop neural self-regulation of alpha activity and visuospatial attention: evidence in favor of a causal role?

Closed-loop neural self-regulation (also known as neurofeedback training) is a procedure in which a continuous brain activity marker (e.g., alpha amplitude) is displayed to the participant in real time. Based on operant conditioning, the aim is to make the participant's brain 'learn' which brain activation level or pattern to produce [28,29]. This approach can be used to test whether posterior alpha amplitude modulation plays a causal role during visuospatial attention shifts. Specifically, if participants are trained to display lateralized posterior alpha activity modulation, similar to the modulation observed during shifts of visuospatial attention, their attentional

(i.e., without moving their eyes). This is followed by the presentation of a visual target stimulus either in the attended visual hemifield (valid trial) or in a smaller proportion of trials in the unattended hemifield (invalid trial).

Steady-state visually evoked potentials (SSVEPs): an ERP (i.e., a neural response observable after averaging neural activity over a large number of trials) elicited by a series of rhythmically displayed visual stimuli, which is characterized by an increase in amplitude and a rhythmic amplitude modulation persisting throughout the stimulation. It is modulated by attentional processing, as indicated by an increase in amplitude in response to attended stimuli relative to unattended stimuli.



processing should be altered accordingly. In a recent study employing this approach [30], participants were trained to either selectively increase left parietal magnetoencephalographic (MEG) alpha activity or right parietal alpha amplitude. In response to neurofeedback training, evoked responses were attenuated in the hemisphere where alpha had been increased and visuospatial attention performance was increased ipsilateral to the hemisphere with increased alpha amplitudes. Neurofeedback training itself had been administered without any lateralized visual task and without a task that required shifting of visuospatial attention [30]. It seems reasonable to conclude that the study provides solid evidence for a causal role of lateralized alpha amplitude modulation in visuospatial attention control.

However, again, counter arguments could be raised. It has been argued that even when using a centrally presented, non-visuospatial-attention-like feedback task during the neurofeedback training, participants might adopt a strategy in which they covertly shift their visual attention to either the left or the right visual hemifield to provoke increased alpha activity ipsilateral (as well as decreased alpha amplitudes contralateral) to the attended hemifield [31]. In that case, during the training session participants might learn to indirectly modulate alpha activity by covertly shifting their visuospatial attention to one side (i.e., attentional biasing of one visual hemifield), which would then lead to decreased alpha activity and increased evoked responses in contralateral posterior brain areas, as well as better attentional performance within this hemifield during the subsequent attention task. In this scenario, it cannot be completely ruled out that alpha amplitude might only be the result of shifted visuospatial attention, rather than the basis thereof.

Alpha-related noninvasive brain stimulation (NIBS) and visuospatial attention: evidence (most likely) in favor of a causal role

One of the most common approaches to test causality in cognitive neuroscience is **NIBS** [32,33]. By applying either transcranial magnetic stimulation (TMS) or transcranial electrical stimulation (tES) in a rhythmical fashion, intrinsic brain oscillations can be entrained or perturbed [34–38]. Empirical studies following this approach provide some evidence that posterior alpha activity is causally involved in the control of visuospatial attention.

In one study, repetitive TMS at 5, 10, or 20 Hz was applied over the parieto-occipital cortex, immediately followed by a visual, near-threshold target shown in the visual field ipsilateral or contralateral to the stimulation [39]. Among the protocols, only 10-Hz stimulation (i.e., stimulation in the alpha frequency range) led to increased detection rates for targets presented ipsilateral to the stimulation site, whereas targets contralateral to the TMS were less likely to be detected. So, **entrainment** of alpha activity by external rhythmical stimulation can have the same effect on visual perception as that found during voluntary shifting of visuospatial attention. By increasing alpha activity in one hemisphere, visual perception is biased towards more efficient information processing in the ipsilateral visual field. There is recent evidence showing a similar effect even during a visuospatial attention task [40]. It was demonstrated that transcranial alternating-current stimulation (tACS) at participants' individual alpha frequency over the left parieto-occipital cortex altered task performance in a spatial cueing paradigm. Entraining (i.e., increasing) alpha activity contralateral to targets led to increased response times in invalidly cued trials. Importantly, this effect was observed only in endogenous shifts of attention and not in exogenous attention trials, supporting the idea that modulation of alpha activity leads to top-down-controlled changes in visual information processing.

Another noninvasive approach to test causality involves reversible, 'virtual' lesions to specific cortical locations. Applying virtual lesions at cortical regions known to be causally involved in the control of visuospatial attention was shown to impact attention-related alpha activity and

task performance. In a study using a **Posner task**, repetitive TMS at 20 Hz (which causes a transient, virtual lesion) applied over the intraparietal sulcus or the frontal eye field (FEF) just following the presentation of a spatial cue led to a collapse of lateralized alpha activity and reduced task performance [41]. Moreover, the TMS-induced change of lateralized attention-related alpha activity predicted response times during the Posner task. Another study found similar results when applying slow repetitive TMS (rTMS) (causing reduced cortical excitability outlasting the stimulation) over the right FEF [42]. The stimulation led to increased response times in valid trials in a Posner task as well as the obliteration of attention-related lateralized alpha activity in the cue–target interval.

It seems reasonable to conclude, then, that posterior alpha activity is a substrate of visuospatial attention: entrainment of alpha activity leads to alterations of attentional task performance that correspond to the location of the activity being manipulated and ‘knocking out’ of lateralized alpha activity using virtual lesions leads to reduced attentional processing. While these lines of research provide evidence for a causal role of alpha modulation in visuospatial attention, the specific ways in which alpha activity might affect cortical processing remain equivocal. An idea of relevance in this context, as discussed later, is that alpha activity might not implement gain control as a neural substrate of cortical excitability in the early visual areas but rather acts as a gating mechanism that controls the flow of low-level information to higher visual areas.

Alpha activity in the early visual areas, parietal cortex, and frontoparietal networks: what is the specific function of alpha activity in visuospatial attention?

As pointed out earlier, it has been suggested that alpha activity represents a mechanism of controlling cortical excitability [10,12,14,43]. This, of course, should also hold for early visual areas. Related to this, it was shown that spontaneous fluctuations in alpha oscillatory activity recorded at occipitoparietal electrode sites predicted the perception of TMS-induced phosphenes [5]. Higher spontaneous pre-stimulation alpha activity representing cortical deactivation led to a reduced probability of perception of phosphenes. In other studies, it was found that the level of occipital alpha activity determined perceptual performance in visual discrimination tasks, with higher alpha amplitude being associated with poorer perception [44–46].

In addition to alpha amplitude, the instantaneous phase and inter-regional coherence of alpha oscillations are important features in the context of attentional phenomena. In particular, short-term fluctuations in perception and attention seem to correlate with phase-based measures of alpha activity. This observation is consistent with the notion that the current phase of an ongoing EEG oscillation reflects a momentary state of the neuronal population’s excitability and is thus indicative of more or less favorable time intervals for successful information processing [47–49]. In a study providing an elegant example of these relationships [50], the processing of near-threshold visual targets was dependent not only on alpha amplitude but also on the alpha phase being in a preferable peak state at target onset, suggesting two supplementary mechanisms based on steady versus pulsed release from alpha-driven inhibition, respectively (see also [10,12,51–53]).

A related point of consideration is the substrates of top-down attentional control. The processes discussed above, of instantaneous alpha-phase-dependent fluctuations in visual perceptual processing, are unlikely to be directly modulated by voluntary top-down control, although they could still be critically involved in the implementation of visuospatial attention [49]. By contrast, a good candidate for top-down attentional control is interregional **phase coherence** [18–20] as a proxy for synchrony and successful communication between neuronal populations [54]. During the cue–target interval in a Posner task, increased frontoparietal alpha phase coherence was observed contralateral to the visual hemifield that attention was shifted towards [3].



Moreover, high frontoparietal alpha coherence was associated with a decreased probability of missing the second of two rapidly presented targets, a phenomenon known as attentional blink, suggesting alpha coherence-dependent tuning of an attentional filter [55]. These findings point towards a vital role of frontoparietal interaction in controlling visuospatial attention and possibly controlling the excitation level of posterior brain areas (indicated by modulated alpha amplitude). Direct evidence for this interpretation comes from a study in which, during an attentional shifting task, the FEF was transiently, virtually lesioned using TMS [42]. As mentioned earlier, this intervention led to reduced modulation of posterior alpha activity. At the same time, the prefrontal drive onto posterior parietal sites at alpha frequency was reduced. Further, this top-down prefrontal-to-parietal coupling reduction predicted interindividual differences in behavioral TMS response in the attention task.

So, does that mean that a frontoparietal attention network [56] synchronized at alpha frequency [18–20,42] controls perceptual gain in the early visual cortex by means of alpha amplitude modulation? Most likely not. As pointed out earlier, SSVEPs in the early visual cortex as a proxy of visual gain control are not correlated with alpha amplitude modulation [22,23]. Also, the FEF does not seem to directly control the excitation level of the early visual cortex, as demonstrated by concurrent TMS and electrophysiological recordings [57]. In a recent MEG study [21], no evidence for alpha oscillations implementing gain control in early visual areas was found. Instead it was suggested that attentional modulation of alpha activity in the parieto-occipital cortex reflected a gating mechanism; that is, alpha activity would be involved in selecting upstream information from early visual areas to be consciously processed. In other words, unlike the classical view, in which alpha power modulations are proposed as an attention mechanism affecting the likelihood of successful information processing in the early visual cortex, alpha power may in fact be involved in a selection process higher up the hierarchy.

This could explain why, for instance, in the study discussed earlier [24] attention effects of alpha activity were found to set in slightly later than initially expected. Gain control in early visual areas might be implemented largely independent of attention-related alpha amplitude modulations in the higher visual cortex (and be reflected by early effects obtained by SSVEPs). Upstream visual information would then be submitted to attentional gating by alpha activity in the higher visual cortex.

How could this suggested gating mechanism be reflected by alpha activity work? As discussed earlier, perceptual processes in the early visual cortex seem tightly tied to the instantaneous alpha phase [50,51,53]. The oscillation might represent a rhythmic fluctuation between excitation and inhibition [6,39], with the inhibitory phase being prolonged by the amplitude increase [12,13] (Figure 2); in other words, if the amplitude increases, the **duty cycle** (i.e., the part of the alpha cycle that is associated with increased neuronal firing [14]) becomes shortened; alpha amplitude suppression, by contrast, would lead to a longer duty cycle. If, therefore, rhythmically sampled pre-attentive perceptual information is fed forward to a parietal cortex that exhibits alpha suppression, the likelihood of this information being further processed in parietal areas is high. If this rhythmically sampled perceptual information, however, meets the parietal cortex at high alpha amplitude (and consequently a short duty cycle), the chances are high that this visual information arrives at a time interval of high inhibition. This perceptual information would, therefore, be blocked from further processing (Figure 2).

Concluding remarks

While alpha activity may represent only one among several mechanisms in attentional processing, it seems reasonable to conclude that it plays a causal role in shifts of visuospatial attention.

Outstanding questions

What are the mechanisms by which remote brain areas (e.g., the prefrontal cortex) impact posterior alpha amplitude modulation?

Which plays a greater role in visuospatial attention processes: alpha amplitude modulation or the instantaneous phase of alpha activity?

What role does the interaction between alpha activity and oscillatory brain processes in other frequency ranges play in the control of visual attention?

Are there further, parallel attentional gating mechanisms beyond alpha frequency; for instance, ones that are reflected by activity in other frequency bands?

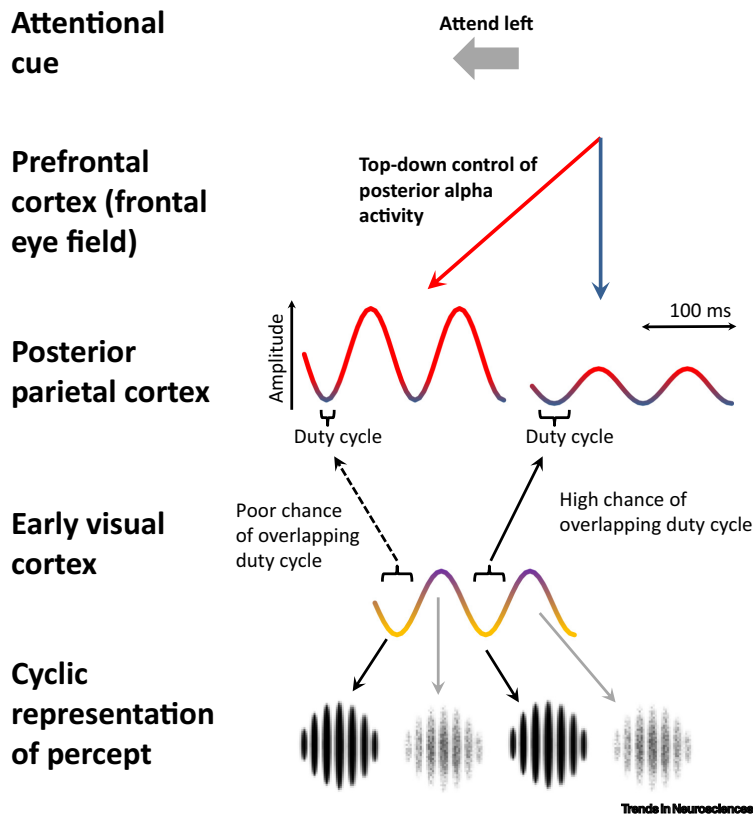


Figure 2. Proposed mechanism by which alpha activity in higher visual areas implements attentional gating. In response to a cue, the prefrontal cortex initiates the modulation of alpha activity in the posterior parietal cortex. The amplitude of the alpha activity will determine the length of the respective duty cycle, with a high amplitude leading to a relatively short duty cycle. At the same time, sensory input is rhythmically sampled at alpha frequency in the early visual cortex. The probability of this upstream information being further processed in the higher visual cortex is increased when the parietal alpha amplitude is low and, therefore, the duty cycle is long. With the very short duty cycle when alpha activity is high, it is likely that in this scenario the rhythmically sampled sensory input will meet the longer inhibitory phase of alpha and consequently will not be further processed.

However, it might not directly implement gain control in the early visual cortex but instead reflect a mechanism higher up the visual hierarchy, possibly attentional gating. There is also good evidence to suggest that alpha activity in higher visual areas is strongly influenced by the prefrontal cortex and frontoparietal attention networks. An analogy to the situation can be drawn from the world of toy cars. To steer a radio-controlled toy car, there is a need for a remote control, a receiver, a servomotor, and a wheel suspension system. Collectively, these elements ultimately point the wheels in a certain direction. Obviously, one would not make the case that any of these parts, the wheels' pointing to the right (for instance), has a causal role in the car taking a right turn. Likewise, posterior alpha activity seems causally involved in visuospatial attention (and most



likely not on a level of the early visual cortex), but only as one part in a multiple-element control mechanism. Future research needs to address, however, the temporal dynamics and context specificity of the attentional gating mechanism implemented by alpha activity (see [Outstanding questions](#)). Prior work has shown, for instance, that preparatory alpha activity seems to be exclusively associated with target cuing and not with distracter cuing [58–60]. These findings are not fully compatible with the idea of alpha activity reflecting a general gating mechanism of attention, giving rise to the assumption that there might even be further, parallel gating mechanisms involved in attention – potentially reflected by oscillatory brain activity beyond alpha frequency.

Acknowledgments

This research was supported by the German Research Council (DFG) (grant SA 1872/2-2).

Declaration of interests

The authors declare no competing interests.

References

- Worden, M.S. *et al.* (2000) Anticipatory biasing of visuospatial attention indexed by retopically specific alpha-band electroencephalography increases over occipital cortex. *J. Neurosci.* 20, RC63
- Thut, G. *et al.* (2006) Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J. Neurosci.* 26, 9494–9502
- Sauseng, P. *et al.* (2005) A shift of visual spatial attention is selectively associated with human EEG alpha activity. *Eur. J. Neurosci.* 22, 2917–2926
- Rihs, T.A. *et al.* (2009) A bias for posterior alpha-band power suppression versus enhancement during shifting versus maintenance of spatial attention. *Neuroimage* 44, 190–199
- Romei, V. *et al.* (2008) Spontaneous fluctuations in posterior alpha-band EEG activity reflect variability in excitability of human visual areas. *Cereb. Cortex* 18, 2010–2018
- Sauseng, P. *et al.* (2009) Spontaneous locally restricted EEG alpha activity determines cortical excitability in the motor cortex. *Neuropsychologia* 47, 284–288
- Neuper, C. *et al.* (2006) ERD/ERS patterns reflecting sensorimotor activation and deactivation. *Prog. Brain Res.* 159, 211–222
- Plurtscheller, G. and Lopes da Silva, F.H. (1999) Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin. Neurophysiol.* 110, 1842–1857
- Hanslmayr, S. *et al.* (2012) Oscillatory power decreases and long-term memory: the information via desynchronization hypothesis. *Front. Hum. Neurosci.* 6, 74
- Klimesch, W. *et al.* (2007) EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res. Rev.* 53, 63–88
- Sauseng, P. *et al.* (2009) Brain oscillatory substrates of visual short-term memory capacity. *Curr. Biol.* 19, 1846–1852
- Jensen, O. and Mazaheri, A. (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.* 4, 186
- Mazaheri, A. and Jensen, O. (2010) Rhythmic pulsing: linking ongoing brain activity with evoked responses. *Front. Hum. Neurosci.* 4, 177
- Haegens, S. *et al.* (2011) α -Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proc. Natl. Acad. Sci. U. S. A.* 108, 19377–19382
- Jäncke, L. *et al.* (2006) Converging evidence of ERD/ERS and BOLD responses in motor control research. *Prog. Brain Res.* 159, 261–271
- Foster, J.J. *et al.* (2016) The topography of alpha-band activity tracks the content of spatial working memory. *J. Neurophysiol.* 115, 168–177
- Foster, J.J. and Awh, E. (2019) The role of alpha oscillations in spatial attention: limited evidence for a suppression account. *Curr. Opin. Psychol.* 29, 34–40
- Sadaghiani, S. *et al.* (2012) α -Band phase synchrony is related to activity in the fronto-parietal adaptive control network. *J. Neurosci.* 32, 14305–14310
- Lobier, M. *et al.* (2018) High-alpha band synchronization across frontal, parietal and visual cortex mediates behavioral and neuronal effects of visuospatial attention. *Neuroimage* 165, 222–237
- Suess, N. *et al.* (2021) Differential attention-dependent adjustment of frequency, power and phase in primary sensory and frontoparietal areas. *Cortex* 137, 179–193
- Zhigalov, A. and Jensen, O. (2020) Alpha oscillations do not implement gain control in early visual cortex but rather gating in parieto-occipital regions. *Hum. Brain Mapp.* 41, 5176–5186
- Keitel, C. *et al.* (2019) Stimulus-driven brain rhythms within the alpha band: the attentional-modulation conundrum. *J. Neurosci.* 39, 3119–3129
- Gundlach, C. *et al.* (2020) Spatial attentional selection modulates early visual stimulus processing independently of visual alpha modulations. *Cereb. Cortex* 30, 3686–3703
- Antonov, P.A. *et al.* (2020) Too little, too late, and in the wrong place: alpha band activity does not reflect an active mechanism of selective attention. *Neuroimage* 219, 117006
- Hillyard, S.A. and Anillo-Vento, L. (1998) Event-related brain potentials in the study of visual selective attention. *Proc. Natl. Acad. Sci. U. S. A.* 95, 781–787
- Slotnick, S.D. (2018) Attentional modulation of early visual areas. *Cogn. Neurosci.* 9, 1–3
- Green, J.J. and McDonald, J.J. (2008) Electrical neuroimaging reveals timing of attentional control activity in human brain. *PLoS Biol.* 6, e81
- Sitaram, R. *et al.* (2017) Closed-loop brain training: the science of neurofeedback. *Nat. Rev. Neurosci.* 18, 86–100
- Jensen, O. *et al.* (2011) Using brain-computer interfaces and brain-state dependent stimulation as tools in cognitive neuroscience. *Front. Psychol.* 2, 100
- Bagherzadeh, Y. *et al.* (2020) Alpha synchrony and the neurofeedback control of spatial attention. *Neuron* 105, 577–587.e5
- Gundlach, C. and Förschack, N. (2020) Commentary: alpha synchrony and the neurofeedback control of spatial attention. *Front. Neurosci.* 14, 597
- Bergmann, T.O. and Hartwigsen, G. (2020) Inferring causality from noninvasive brain stimulation in cognitive neuroscience. *J. Cogn. Neurosci.* 33, 195–225
- Taylor, P.C.J. (2018) Combining NIBS with EEG: what can it tell us about normal cognition? *Curr. Behav. Neurosci. Rep.* 5, 165–169
- Taylor, P.C.J. and Thut, G. (2012) Brain activity underlying visual perception and attention as inferred from TMS-EEG: a review. *Brain Stimul.* 5, 124–129

Trends in Neurosciences



35. Thut, G. and Miniussi, C. (2009) New insights into rhythmic brain activity from TMS-EEG studies. *Trends Cogn. Sci.* 13, 182–189
36. Herrmann, C.S. *et al.* (2016) EEG oscillations: from correlation to causality. *Int. J. Psychophysiol.* 103, 12–21
37. Hanslmayr, S. *et al.* (2019) Modulating human memory via entrainment of brain oscillations. *Trends Neurosci.* 42, 485–499
38. Thut, G. *et al.* (2011) Rhythmic TMS causes local entrainment of natural oscillatory signatures. *Curr. Biol.* 21, 1176–1185
39. Romei, V. *et al.* (2010) On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? *J. Neurosci.* 30, 8692–8697
40. Kasten, F.H. *et al.* (2020) Hemisphere-specific, differential effects of lateralized, occipital-parietal α - versus γ -TACS on endogenous but not exogenous visual–spatial attention. *Sci. Rep.* 10, 12270
41. Capotosto, P. *et al.* (2009) Frontoparietal cortex controls spatial attention through modulation of anticipatory alpha rhythms. *J. Neurosci.* 29, 5863–5872
42. Sauseng, P. *et al.* (2011) Right prefrontal TMS disrupts interregional anticipatory EEG alpha activity during shifting of visuospatial attention. *Front. Psychol.* 2, 241
43. Klimesch, W. (2012) α -Band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* 16, 608–617
44. Hanslmayr, S. *et al.* (2007) Prestimulus oscillations predict visual perception performance between and within subjects. *Neuroimage* 37, 1465–1473
45. Hanslmayr, S. *et al.* (2005) Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neurosci. Lett.* 375, 64–68
46. Michail, G. *et al.* (2021) Prestimulus alpha power but not phase influences visual discrimination of long-duration visual stimuli. *Eur. J. Neurosci.* Published online March 5, 2021. <https://doi.org/10.1111/ejn.15169>
47. Berger, B. *et al.* (2014) EEG oscillatory phase-dependent markers of corticospinal excitability in the resting brain. *Biomed. Res. Int.* 2014, 936096
48. Buzsáki, G. and Draguhn, A. (2004) Neuronal oscillations in cortical networks. *Science* 304, 1926–1929
49. Zoefel, B. and VanRullen, R. (2017) Oscillatory mechanisms of stimulus processing and selection in the visual and auditory systems: state-of-the-art, speculations and suggestions. *Front. Neurosci.* 11, 296
50. Mathewson, K.E. *et al.* (2009) To see or not to see: prestimulus alpha phase predicts visual awareness. *J. Neurosci.* 29, 2725–2732
51. Busch, N.A. and VanRullen, R. (2010) Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proc. Natl. Acad. Sci. U. S. A.* 107, 16048–16053
52. Palva, S. and Palva, J.M. (2007) New vistas for alpha-frequency band oscillations. *Trends Neurosci.* 30, 150–158
53. Spaak, E. *et al.* (2014) Local entrainment of α oscillations by visual stimuli causes cyclic modulation of perception. *J. Neurosci.* 34, 3536–3544
54. Fries, P. (2015) Rhythms for cognition: communication through coherence. *Neuron* 88, 220–235
55. Glennon, M. *et al.* (2016) Distributed cortical phase synchronization in the EEG reveals parallel attention and working memory processes involved in the attentional blink. *Cereb. Cortex* 26, 2035–2045
56. Corbetta, M. and Shulman, G.L. (2011) Spatial neglect and attention networks. *Annu. Rev. Neurosci.* 34, 569–599
57. Veniero, D. *et al.* (2021) Top-down control of visual cortex by the frontal eye fields through oscillatory realignment. *Nat. Commun.* 12, 1757
58. Noonan, M.P. *et al.* (2016) Distinct mechanisms for distractor suppression and target facilitation. *J. Neurosci.* 36, 1797–1807
59. Noonan, M.P. *et al.* (2018) Selective inhibition of distracting input. *Behav. Brain Res.* 355, 36–47
60. Schneider, D. *et al.* (2021) Target enhancement or distractor suppression? Functionally distinct alpha oscillations form the basis of attention. *Eur. J. Neurosci.* Published online October 7, 2020. <https://doi.org/10.31234/osf.io/df23g>
61. Breitzynski, J.A. and DeYoe, E.A. (1999) A physiological correlate of the “spotlight” of visual attention. *Nat. Neurosci.* 2, 370–374

Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation

- **Hilla, Y.**, Von Mankowski, J., Föcker, J., & Sauseng, P. (2020). Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation. *Frontiers in Psychology, 11*, 599788.
- **Y.H.:** Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Project Administration, Software Development, Writing - Review & Editing. **J.M.:** Software Development, Writing - Review & Editing. **J.F.:** Conceptualization, Validation, Writing - Review & Editing. **P.S.:** Conceptualization, Funding Acquisition, Resources, Validation, Writing - Review & Editing.
- I developed the experimental design of this study. This included a comprehensive literature research and developing software to run the task. Moreover, I personally conducted the research. Furthermore, I analyzed the data and performed statistical tests. Furthermore, I wrote the the manuscript to summarize the results of our research, and reviewed and edited the manuscript. Also, I took care of data curation, e.g., anonymization, etc.



Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation

Yannik Hilla¹, Jörg von Mankowski², Julia Föcker³ and Paul Sauseng^{1*}

¹ Research Unit of Biological Psychology, Department of Psychology, Ludwig-Maximilians-Universität München, Munich, Germany, ² Chair of Communication Networks, Technische Universität München, Munich, Germany, ³ School of Psychology, College of Social Sciences, University of Lincoln, Lincoln, United Kingdom

Video gaming, specifically action video gaming, seems to improve a range of cognitive functions. The basis for these improvements may be attentional control in conjunction with reward-related learning to amplify the execution of goal-relevant actions while suppressing goal-irrelevant actions. Given that EEG alpha power reflects inhibitory processing, a core component of attentional control, it might represent the electrophysiological substrate of cognitive improvement in video gaming. The aim of this study was to test whether non-video gamers (NVGs), non-action video gamers (NAVGs) and action video gamers (AVGs) exhibit differences in EEG alpha power, and whether this might account for differences in visual information processing as operationalized by the theory of visual attention (TVA). Forty male volunteers performed a visual short-term memory paradigm where they memorized shape stimuli depicted on circular stimulus displays at six different exposure durations while their EEGs were recorded. Accuracy data was analyzed using TVA-algorithms. There was a positive correlation between the extent of post-stimulus EEG alpha power attenuation (10–12 Hz) and speed of information processing across all participants. Moreover, both EEG alpha power attenuation and speed of information processing were modulated by an interaction between group affiliation and time on task, indicating that video gamers showed larger EEG alpha power attenuations and faster information processing over time than NVGs – with AVGs displaying the largest increase. An additional regression analysis affirmed this observation. From this we concluded that EEG alpha power might be a promising neural substrate for explaining cognitive improvement in video gaming.

Keywords: theory of visual attention (TVA), attentional control, short-term memory, learning to learn, cognitive improvement in video gamers, knowledge system

OPEN ACCESS

Edited by:

Mannes Poel,
University of Twente, Netherlands

Reviewed by:

Benjamin Cowley,
University of Helsinki, Finland
Andreea Ioana Sburlea,
Graz University of Technology, Austria

*Correspondence:

Paul Sauseng
paul.sauseng@lmu.de

Specialty section:

This article was submitted to
Human-Media Interaction,
a section of the journal
Frontiers in Psychology

Received: 28 August 2020

Accepted: 04 November 2020

Published: 08 December 2020

Citation:

Hilla Y, von Mankowski J, Föcker J
and Sauseng P (2020) Faster Visual
Information Processing in Video
Gamers Is Associated With EEG
Alpha Amplitude Modulation.
Front. Psychol. 11:599788.
doi: 10.3389/fpsyg.2020.599788

INTRODUCTION

There is convincing evidence that playing commercially available video games, in particular action video games, such as Battlefield V (EA DICE; Stockholm), may improve cognitive functions – ranging from perception (Dye et al., 2009; Li et al., 2009, 2010; Bejjanki et al., 2014), over memory (Blacker and Curby, 2013; Blacker et al., 2014; McDermott et al., 2014; Pavan et al., 2019), probabilistic inference (Green et al., 2010; Schenk et al., 2017), and executive control (Colzato et al., 2010; Cain et al., 2012; Green et al., 2012; Strobach et al., 2012) to attentional deployment

(Greenfield et al., 1994; Green and Bavelier, 2003; Chisholm and Kingstone, 2012; Cain et al., 2014; Wu and Spence, 2013). Thus, video gaming might represent a promising tool both for investigating human learning and therapeutic use in clinical populations (e.g., in patients with amblyopia, see Gambacorta et al., 2018). In this sense, for instance, EndeavorRx™ (Akili Interactive Labs, Boston, MA, United States), a racing video game customized to treat children with ADHD (Kollins et al., 2020), was approved by the Food and Drug Administration (FDA), recently.

However, in order to apply commercially available video games (e.g., Battlefield V) for such purposes, the mechanisms underlying their effects need to be understood more in detail: one prominent attempt to explain how in particular action video games may improve cognitive processing is the idea that they affect one specific cognitive domain which several cognitive functions have in common – also known as learning to learn approach (Bavelier et al., 2012b; Green and Bavelier, 2012). According to this approach (Bavelier et al., 2012b; Green and Bavelier, 2012), playing action video games may improve video gamers' probabilistic inference, which may enhance additional cognitive processes that rely on probabilistic inference, e.g., perception (Deroy et al., 2016) and attention (Rao, 2005). Thus, action video gamers (AVGs) might not outperform non-video gamers (NVGs) in a paradigm right from the start but after a time course of learning. Recently this approach has been developed further as a significant body of research indicated that foremost cognitive functions related to top-down attentional deployment were affected by video gaming (Bediou et al., 2018; Bavelier and Green, 2019). Hereby, Bavelier and Green (2019) suggested that the conjunction between reward-related learning and attentional control might be a core mechanism underlying improvements in cognitive processing related to video gaming. The idea here was that video gaming might train video gamers to select goal-relevant actions over goal-irrelevant actions which, in turn, might lead to more efficient cognitive processing. The basis for this was supposed to be an increase in dopaminergic transmission as video games seem to elicit learning mechanisms similar to operant conditioning, and an enhanced suppression of irrelevant information processing while relevant information processing may be facilitated – which is considered as attentional control in this context (Bavelier and Green, 2019).

In support of this, Koepp et al. (1998) showed that dopaminergic transmission of the left striatum increased during action video gaming; and Kühn et al. (2011) found that adolescents who frequently played video games exhibited larger gray matter volumes and stronger blood oxygenation level dependent signals in the left ventral striatum compared to adolescents with irregular gaming behavior while performing the Monetary Incentive Delay Task. Furthermore, Tanaka et al. (2013) elaborated that AVGs showed larger gray matter volumes in the right posterior parietal cortex than NVGs, and Bavelier et al. (2012a) as well as Föcker et al. (2018) demonstrated that AVGs exhibited different blood oxygenation level dependent signals in brain areas of a dorsal fronto-parietal top-down attention network (Corbetta et al., 2008) compared to NVGs, while performing attention demanding paradigms. Moreover,

AVGs were shown to suppress distractors more efficiently than NVGs and NAVGs as reflected by stronger modulations of steady-state visual evoked potentials in the electroencephalogram (EEG) (Mishra et al., 2011; Krishnan et al., 2013); and, they showed stronger attention related amplitude responses in event-related potentials in the EEG compared to NVGs, for instance, in the anterior N1, P2, and P3 (Wu et al., 2012; Föcker et al., 2019).

However, these neural signatures were mostly (if at all) associated with modulations of attentional deployment, but rarely with modulations in additional cognitive functions (but see also, Tanaka et al., 2013). Thus, these data do not really allow any conclusions as to whether inter-individual differences in these neural substrates may also functionally apply to other cognitive processes. One promising candidate to fill this gap and relate inter-individual differences in neural signatures of attentional control with modulations in additional cognitive functions may be brain oscillatory activity in the frequency range from 8 to 14 Hz – also known as alpha oscillations. According to the inhibition-timing hypothesis (Klimesch et al., 2007b), amplitude modulations of EEG alpha oscillations represent a neural substrate of top-down inhibitory processing (for a validation of and new vistas on the inhibition-timing hypothesis, see also Jensen and Mazaheri, 2010; Fries, 2015). More specifically, the inhibition-timing hypothesis suggests that an increase in EEG alpha power after processing sensory information [also known as event-related synchronization (ERS)] goes along with an increase in inhibitory processing; while a decrease in EEG alpha power after processing sensory information [also known as event-related desynchronization (ERD)] may go along with disinhibition (see also Pfurtscheller and Lopes da Silva, 1999). Inhibitory processing, in turn, is a core property of attention (Chun et al., 2011). Therefore, modulations in EEG alpha power are assumed to represent a neural substrate of attentional control (Klimesch, 2012). Crucially, such modulations were shown to play a considerable role in cognitive functions associated with attentional control – for instance, in perception (Klimesch et al., 2011), (visual short-term) memory (Sauseng et al., 2009; Nenert et al., 2012), executive control (Sauseng et al., 2006), and probabilistic inference (Spaak et al., 2016). Hence EEG alpha power modulations represent a promising candidate for investigating neural mechanism of cognitive improvement related to video gaming. However, in this regard, it needs to be considered that alpha oscillatory activity is highly task-dependent (Klimesch et al., 2011): for instance, while EEG alpha power seems to decrease in anticipation of the time point (Nobre and van Ede, 2018), spatial position (Spaak et al., 2016) or identity (Capotosto et al., 2009) of an up-coming target in visual detection paradigms; it tends to increase in anticipation of stimuli in visual short-term memory paradigms and decrease after stimulus processing later on (e.g., Nenert et al., 2012). Moreover, in line with the inhibition-timing hypothesis, alpha activity tends toward increasing in response to distractors (Worden et al., 2000; Sauseng et al., 2009). Furthermore, EEG alpha oscillations can be sub-divided into lower alpha frequency bands (e.g., from 6.42 to 9.75 Hz, see Freunberger et al., 2008) that seem to be related merely to attentional processing, and medium or upper alpha frequency bands (e.g., from 9.17 to 13 Hz, see

Freunberger et al., 2008) that appear to be correlated with higher level cognitive processing, e.g., when attention is deployed in concert with perception and memory (Klimesch, 1997, 2012; Klimesch et al., 2011). But, the frequency range of lower, medium and upper alpha bands may drastically vary depending on data recording and analysis protocols.

Hazarika et al. (2018) and Hazarika and Dasgupta (2020) have already provided some evidence that AVGs might exhibit differences in EEG alpha oscillatory activity as they found that AVGs showed larger relative EEG alpha power values than NVGs while performing a Corsi block-tapping task and the Bivalent Shape Task. But their results should be considered with caution as their procedures to estimate participant's relative EEG alpha power values was problematic. One of the main issues here may be that each participant's relative EEG alpha power value was estimated based on trials of different lengths, while performing the Corsi block-tapping task since the length of a trial depended on the individual performance of a participant (Hazarika and Dasgupta, 2020). Thus, the estimates are hardly comparable between subjects and groups. On top of that, it appeared that Hazarika et al. (2018) and Hazarika and Dasgupta (2020) did not control for potential contaminations by stimulus exposure duration, time on task or task requirements, though EEG alpha power was shown to decay over time, to be modulated by time on task and to be highly task-specific (Klimesch et al., 2011; Benwell et al., 2019). Furthermore, they reported relative EEG alpha power estimates that were quite broad (7.8–15.6 Hz). Thus, the estimates might reflect the impact of not only alpha oscillatory activity but also other frequency bands. In conclusion, further research on the functional role of EEG alpha oscillatory activity in inter-individual differences in cognitive processing between video gamers and control participants is required to understand neural mechanisms underlying cognitive improvements due to video gaming.

In this regard, the aim of this study was to investigate whether habitual gaming behavior might modulate EEG alpha power while processing stimuli in a visual-short-term memory paradigm, and whether such modulations might be relatable to inter-individual differences in visual attentional information processing. For this, we applied a computational modeling approach based on the theory of visual attention (TVA; Bundesen, 1990; Bundesen et al., 2015) because it allows the computation of several parameter values associated with visual attentional processing, such as speed of information processing (C) or the maximum capacity of the visual short-term memory store (K) (Kyllingsbaek, 2006; Dyrholm et al., 2011). For this, participants' accuracy data are fit to exponential graphs using TVA-algorithms to determine their TVA C and K parameter values based on the assumptions (1) that the capacity of the visual short-term memory store is limited, (2) but that all visual information is processed in parallel and (3) hence needs to be filtered according to subjectively relevant criteria using attentional deployment. Hereby, the y -asymptotic levels of the exponential graphs represent K parameter values and slope lines that intersect the exponential graph on the x -axis C parameter values. We decided on investigating TVA C and K parameter values in particular since they were likely related with EEG alpha activity

as they have been associated with the posterior N1 and the contralateral delay activity (CDA), respectively (Wiegand et al., 2014b) – two event-related potentials that have been discussed to be linked to EEG alpha activity (Klimesch et al., 2004; Gruber et al., 2005; Klimesch et al., 2007a; van Dijk et al., 2010); and because ERD in the medium or upper alpha frequency band is considered a crucial neural signature in visual short-term memory (Klimesch, 1997, 2012; Sauseng et al., 2009; Nenert et al., 2012). An additional reason was that video gamers were shown to exhibit larger TVA C parameter values than NVGs (Wilms et al., 2013) – an effect already replicated (Schubert et al., 2015). Hence, the effect was considered suitable to investigate whether inter-individual differences in event-related EEG alpha power modulations between video gamers and NVGs might predict differences in TVA C parameter values – but not in TVA K parameter values since video gamers and NVGs did not seem to differ in the capacity of visual short-term memory as operationalized by the TVA K parameter (Wilms et al., 2013; Schubert et al., 2015).

Therefore, we hypothesized (1) that the extent of participants' ERD in the medium or upper alpha frequency band after processing stimuli presented in a visual short-term memory paradigm may be correlated with TVA C and K parameter values, respectively; (2) that habitual video gaming might modulate EEG alpha power as video gaming seems to impact on attentional control; and (3) that inter-individual differences in ERD in the medium or upper alpha frequency bands between video gamers and non-video gamers might go along with inter-individual differences in TVA C parameter values. On top of that, we expected (4) that different lengths of exposure durations used to compute TVA parameter values and time on task as operationalized by experimental blocks in our paradigm might contaminate our EEG alpha power estimates – which is why we controlled for these factors in our statistical analyses (Klimesch et al., 2011; Benwell et al., 2019).

MATERIALS AND METHODS

Participants

We recruited participants via flyers published on mailing lists and internet platforms, stating that we were looking for male volunteers to participate in an EEG study on perceptual processing. Thus, we did not explicitly recruit video gamers, but we used a cover story to prevent selection bias and expectation effects from confounding the data (Boot et al., 2011; Schubert and Strobach, 2012).

A screening was conducted to control whether prospective volunteers were suitable for participating in the study. Only male individuals between 18 and 40 years of age with normal or corrected-to-normal vision and no history of neurological or psychiatric disorders were eligible. We recruited only male participants as their representation among video gamers was likely larger than that of females (Entertainment Software Association, 2019) – a procedure which is quite common in gaming research (e.g., Green and Bavelier, 2007). In total 40 healthy male German- or English-speaking volunteers with

normal or corrected-to-normal vision participated in our study. Fifteen were classified as NVGs, 15 as NAVGs and 10 as AVGs. The data of two participants were excluded due to poor EEG data quality. Thus, data of 14 NVGs ($M_{\text{age}} = 24.93$ years, age range = 22–30 years), 15 NAVGs ($M_{\text{age}} = 22.73$ years, age range = 19–32 years) and 9 AVGs ($M_{\text{age}} = 24.89$ years, age range = 21–31 years) were used for statistical analyses. Our sample size was comparable to sample sizes reported in studies that followed a similar methodological approach (Wilms et al., 2013; Schubert et al., 2015), and in studies investigating other gaming effects (Li et al., 2009, 2011; Wu et al., 2012). The three groups did not differ in mean age, $F(2,35) = 2.43$, $p = 0.103$, and were similar in educational status (High School graduation vs. Bachelor's Degree vs. Master's Degree vs. German Diploma, Fisher's exact test, $p = 0.128$). The study was approved by the local ethics review board. All volunteers gave written informed consent in accordance with the Declaration of Helsinki before their participation, and they were compensated with 3 Euros for participating in the screening and 10 Euros per hour spent on the EEG study, or participants received student lab tokens.

Procedures and Materials

Video Gaming Questionnaire

Prior to testing, we asked participants to provide the names of a maximum of 10 video games they had played regularly and most often in the previous 12–24 months. In addition to that, we asked how many hours per week they had played the respective games on average in the previous 12–24 months. Each video game's genre was determined based on the producers' description. With regard to the classification scheme of Green et al. (2017), subjects were, then, classified as NVGs if in the previous 12–24 months, they had played first/third person shooter, action role play/adventure, sports/driving, real-time strategy/multi-player online platform video games each for a maximum of 1 h and non-action turn-based role play/fantasy, turn-based strategy/life simulation/puzzle, music or other video games each for a maximum of 3 h, but in total not more than 5 h per week on average. Participants were classified as AVGs if in the previous 12–24 months, they had played first/third person shooter, action role play/adventure games for at least 5 h per week on average. All remaining individuals were classified as NAVGs.

Visual Short-Term Memory Paradigm

Our paradigm was run on a computer with an AMD Athlon™ II X2 B24 processor (AMD, Sunnyvale, CA, United States) and a 64-Bit Windows 7 operating system (Microsoft, Redmond, WA, United States). The paradigm was developed using Python's (Version 3.7.3; Python Software Foundation) Tkinter library¹ and run in Spyder (Version 3.3.3²). Stimuli were presented on a 17"/43 cm monitor (Acer Group, Taiwan) with a refresh rate of 60 Hz. Triggers were sent to the EEG computer using the *dportio.dll in-script plug-in*.³ Responses were given on a

regular keyboard (KB212-B; Dell Technologies Inc., Round Rock, United States).

We developed our own TVA paradigm based on Vangkilde et al. (2011) with shape stimuli instead of letter stimuli to control for language confounds. Participants sat in a comfortable chair, approximately 80 cm from the screen, in a dimly lit room. Each trial started with the presentation of a gray blank screen. After 1002 ms, a white fixation cross was depicted in the center of the screen ($0.72^\circ \times 0.72^\circ$ of visual angle). After an additional 1002 ms, a stimulus display comprising 6 out of 10 white geometrical shapes (circle, ellipse, hexagon, diamond, pentagon, rhombus, square, star, trapezoid, triangle) was presented. Those shapes were displayed on an invisible circle at 30° , 90° , 150° , 210° , 270° and 330° around the fixation cross. The radius of the circle was 2.72° of visual angle. Each shape was located within an area of $2.29^\circ \times 2.29^\circ$ of visual angle and could reach a maximum size of $2.08^\circ \times 2.08^\circ$ of visual angle (e.g., square). Stimulus displays were presented at one of six different exposure durations (16.7, 33.4, 50.1, 83.5, 150.3, and 200.4 ms). Directly after the stimulus display, a mask display consisting of white squares of $2.29^\circ \times 2.29^\circ$ of visual angle with random black polygons based on 8 random points was presented to interrupt processing of stimulus displays exactly at the end of the exposure duration. This mask display lasted for 501 ms. Thereafter, an instruction written in white letters was displayed in the center of the screen. Participants were asked to retrieve as many shapes as possible and to indicate which ones had been presented by pressing corresponding buttons on the keyboard (D: circle, F: ellipse, G: hexagon, H: diamond, J: pentagon, K: rhombus, C: square, V: star, B: trapezoid, N: triangle). Each key was marked with a glow-in-the-dark sticker of the corresponding shape. Participants were asked not to guess. Every new trial was initiated by pressing the space bar. Participants started the paradigm with a training block consisting of 24 trials. During this training, participants received feedback. If at least one response was incorrect within a trial, a black "X" covering $0.93^\circ \times 0.93^\circ$ of visual angle was presented in the center of the screen for 501 ms. There were 210 stimulus displays, see equation (1) for details:

$$\frac{10!}{(10-6)! * 6!} = 210 \quad (1)$$

Each stimulus display was presented once in an experimental block and 24 out of those 210 stimulus displays were randomly chosen for the training block. Thus, each participant performed one training block and two experimental blocks, which makes a total of 444 trials. During the training, each exposure duration was used four times and during each experimental block, each exposure duration was used 35 times. The sequence of trials was always random. The association between a stimulus display and an exposure duration was random. Participants were allowed to take a break between blocks and after each trial. For a scheme of an exemplary trial, see Figure 1.

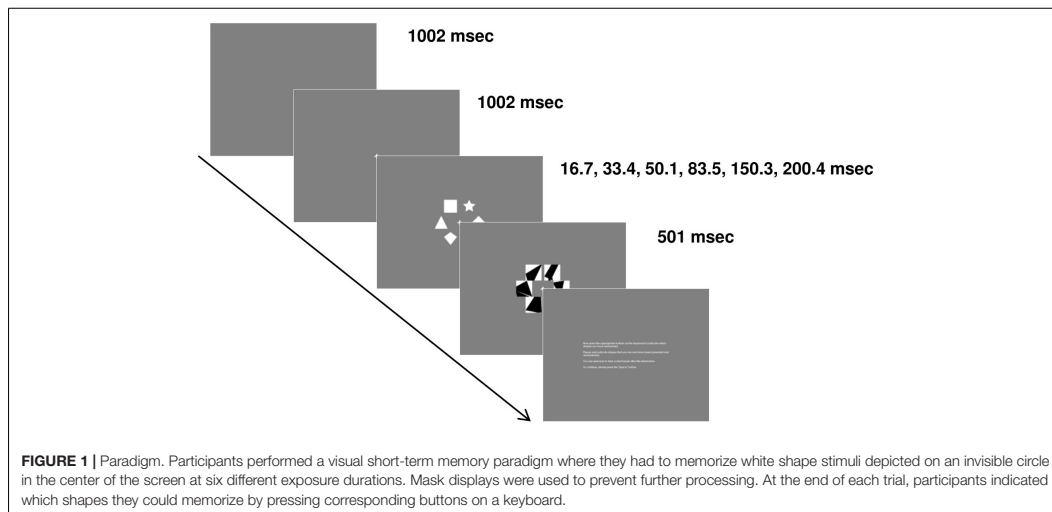
Computation of TVA C and K Parameter Values

Estimating TVA C and K parameter values requires the manipulation of the exposure duration and the application of masks. Manipulating the exposure duration is necessary

¹<https://wiki.python.org/moin/TkInter>

²<https://www.spyder-ide.org/>

³https://real.kyiv.ua/avreal/download/#DLPORTIO_TABLE



because TVA-algorithms estimate each participant's TVA C and K parameter value by fitting their accuracy data at each exposure duration to an exponential distribution by using maximum-likelihood method. Hereby, the slope line that intersects the exponential graph on the x -axis reflects the value of the C parameter, and the y -asymptotic level of the exponential graph reflects the K parameter value (Bundesen, 1990; Kyllingsbaek, 2006; Dyrholm et al., 2011; Bundesen et al., 2015). The application of masks was necessary to prevent visual aftereffects that may otherwise have influenced stimulus processing (see Kyllingsbaek, 2006). As the exposure durations were such an essential element in the computation of TVA C and K parameter values, we inspected the temporal dynamics of the stimuli by using the `default_timer()` function of the `timeit` library⁴. Specifically, we recorded the time points when the in-script commands to visualize stimuli (fixation cross, stimulus displays, mask displays and instruction texts) were given (with a resolution of at least 1 ms) and computed the time differences between them. This, however, revealed that there had been minor imprecisions in the presentation times of the stimuli. Such imprecisions are unfortunately inevitable when using non-real time operating systems and working with a refresh-rate of 60 Hz. We corrected for those flaws by adding the mode value (rounded to the first decimal place) of each exposure duration's deviation distribution to the expected exposure duration value. Thus, we changed the original exposure durations from 16.7, 33.4, 50.1, 83.5, 150.3, and 200.4 ms to 17.8, 35.6, 53.4, 89, 144.6, and 198 ms, respectively. We decided to add the mode value because it represents the most common realization of a distribution and therefore, arguably covers the most frequent exposure durations participants were confronted with while performing the paradigm. We then estimated each participant's TVA C and K parameter value based

⁴<https://docs.python.org/3.7/library/timeit.html>

on their accuracy data of the experimental trials by using the *LIBTVA toolbox* (Dyrholm et al., 2011) run in Matlab R2015a (Math Works, Natick, MA, United States). Finke et al. (2005) established that a minimum of 192 trials in a visual short-term memory paradigm would be sufficient to reliably estimate TVA C and K parameter values in 35 participants. Our visual short-term memory paradigm was comparable to the experimental design used in Finke et al.'s (2005) study and our participants performed 420 experimental trials. Therefore, we were confident that our TVA C and K parameter estimates were reliable.

EEG Data Recording

EEG recordings were stored on a computer with an AMD Athlon™ 64 × 2 Dual Core Processor 5000 + processor (AMD, Sunnyvale, CA, United States) and a 64-Bit Windows 7 operating system (Microsoft, Redmond, WA, United States). EEGs were recorded by using a 64-channel BrainAmp DC amplifier and *Brain Vision Recorder Software* (Brain Products GmbH, Gilching, Germany). Sixty two Ag/AgCl electrodes mounted in a cap (EASYCAP, Herrsching, Germany) were arranged according to the 10–10 international EEG system. During recording, EEGs were referenced against the tip of the nose. Vertical and horizontal EOGs were mounted above the left eyebrow and on the left canthus of the left eye, respectively. EEGs were digitized with a sampling rate of 1000 Hz and filtered with a band-pass filter between 0.016 and 250 Hz. Impedances were kept below 10 kOhm.

Computation of EEG Alpha Power

EEG data were analyzed using *Brain Vision Analyzer 2* (BVA, Brain Products GmbH, Gilching, Germany). At first, raw data were inspected for large scale artifacts such as movement artifacts and artifacts caused by cable movements. Those artifacts were then manually excluded from further analysis using BVA's *Raw*

Data Inspection tool. Subsequently, a bandpass filter between 0.1 and 120 Hz and a notch filter of 50 Hz were applied to reduce slow voltage drifts, muscle artifacts and line noise. If necessary, bad channels were interpolated using the *Topographic Interpolation tool*. Afterward, the EEG was re-referenced to averaged common reference. Then, an *Ocular Correction ICA* was applied using the *Infomax Restricted Algorithm* to correct eye movement artifacts, such as blinks and saccades. After that, a second data inspection was conducted to exclude remaining muscle artifacts, uncorrected EOG artifacts and unspecific spikes. Data were resampled to 1024 Hz to prepare the data for an upcoming *Fast Fourier Transformation* with a resolution of 2 Hz. Data were segmented into segments of 500 ms before the presentation of stimulus displays and after the presentation of the mask display. Subsequently, Fast Fourier Transformation was applied to segments. Trials were then averaged into power spectra for each time window (pre-stimulus and post-mask) and each participant, separately. Then, EEG power ratios were computed by dividing average power spectra before stimulus presentation by average power spectra after mask presentation, see equation (2):

$$\text{EEG power ratio} = \frac{\text{average EEG Power Spectra}_{\text{pre-stimulus}}}{\text{average EEG Power Spectra}_{\text{post-mask}}} \quad (2)$$

Afterward, we achieved *medium and upper alpha ratios* by exporting ratios averaged over occipital, parietal and occipitoparietal channels (O1, O2, Oz, P1, P2, P3, P4, P5, P6, P7, P8, PO3, PO4, PO7, PO8, POz, Pz) of frequency bands ranging from 10–12 and 12–14 Hz. At last, we log-transformed these medium and upper alpha ratios using \log_{10} to prepare the data for statistical analyses based on general linear models. Ratio values > 0 indicated ERD, ratio values < 0 ERS.

We did not include segments ranging from the onset of stimulus displays to the onset of mask displays since we assumed that differences in the exposure durations might contaminate the EEG as they cause different on- and offset evoked potentials. In previous research, this issue was circumvented by combining data of two paradigms – one where masks had been applied but no EEG was recorded and one where masks were not applied but EEGs were recorded (Wiegand et al., 2014a,b, 2016). This procedure certainly allowed for a valid estimation of both TVA parameter values and event-related potentials. However, the shortcoming here may be that an association between the two components might be problematic because of both the temporal distinct recording times and the different task requirements. In contrast, to circumvent this issue, but with the shortcoming of having to neglect data ranging from the presentation of the stimulus display to the presentation of the mask display, we compared alpha power before stimulus processing with alpha power after mask processing. Note also that Hanslmayr et al. (2009) showed that estimates of alpha power modulations were quite stable at the rate of 15 trials and more using a simulation approach (see supplements of Hanslmayr et al., 2009). We used 35 trials to compute alpha power ratios for each exposure duration per block. Therefore, we were confident that our alpha ratios were reliable.

Statistical Analyses

We used *R* (R Core Team, 2018) to conduct statistical analyses and visualize results. Specifically, we used the *apaTables package* to generate tables (Standley, 2018); the *BayesFactor package* to compute Bayes factors (Moray and Rouder, 2018); the *cowplot*, the *ggplot2*, and the *RColorBrewer packages* to visualize data with colorblind-friendly color palettes (Neuwirth, 2014; Wickham, 2016; Wilke, 2019); the *dplyr package* (Wickham et al., 2019) to process data; the *ez package* to compute variance analytical procedures (Lawrence, 2016); the *performance package* to control model assumptions of regression and correlation models (Lüdtke et al., 2020); the *rstatix package* to control model assumptions of variance analytical procedures (Kassambara, 2020); and the *stats package* to conduct Pearson's moment correlation tests. For variance analytical methods with between-subjects factors, we used *Shapiro-Wilk test* (Shapiro and Wilk, 1965) and *Levene's test* (Levene, 1960) to control for assumptions of normality and variance homogeneity, respectively. In case of violations of normality, we, nevertheless, computed variance analytical methods since they were shown to be robust against such violations (Schmider et al., 2010). The assumption of homogeneity was met in all variance analytical models with between-subjects factors. For variance analytical methods with an additional within-subject factor, Mauchly's tests were used to test the assumption of sphericity. In case of a violation of the assumption of sphericity, the *Greenhouse-Geisser correction* was applied (Abdi, 2010). In general, we computed variance analytical procedures based on type II sums of squares since our group sample sizes were unbalanced (Langsrud, 2003). To quantify significant variance analytical results, we reported *generalized eta squared* (η^2_G ; Olejnik and Algina, 2003). For regression and correlation models, we first screened for outliers using *Cook's distance* (Cook, 1977), then the assumptions of normality and of homoscedasticity were controlled. All our regression and correlation models met the assumptions of normality and homoscedasticity. To quantify the strengths of significant associations, we reported Pearson's correlation coefficient r ; and to quantify model fits of regression models, we reported the determination coefficient R^2 . Besides, we computed and reported Bayes factors. These indicate how likely the data occur either under the assumption of H_1 or H_0 . For instance, a Bayes factor $BF_{10} = 4$ indicates the data are four times more in support of the H_1 than the H_0 . In contrast, a Bayes factor $BF_{01} = 3$ indicates the data are three times more in support of the H_0 than the H_1 . We only computed Bayes factors for significant results. We corrected for multiple comparisons using *Bonferroni method* (Bland and Altman, 1995).

At first, we computed 4 one-tailed Pearson's moment correlation tests with average medium or upper alpha ratios and TVA C or K parameter values as variables. We expected positive correlation coefficients as we hypothesized that each participant's ERD in the medium or upper alpha frequency band may be correlated with their TVA C and K parameter values, respectively. For this, we had to average each participant's medium and upper alpha ratio over each level of exposure duration across all blocks to achieve one average medium and upper alpha ratio that could be matched with each participant's individual TVA C and

K parameter value. Note, however, that this was problematic since EEG alpha power might decay over time (Klimesch et al., 2011) – thus, average medium or upper alpha ratios might be contaminated by different lengths of exposure durations; and, EEG alpha power is modulated by time on task (Benwell et al., 2019) – thus, average medium or upper alpha ratios might differ at least between blocks. Afterward, we computed two three-way ANOVAs with GROUP (NVGs vs. NAVGs vs. AVGs) as between-subjects factor, EXPOSURE DURATION (17.8, 35.6, 53.4, 89, 144.6, and 198 ms) and TIME ON TASK (Block 1 vs. Block 2) as within-subject factors and medium and upper alpha ratios as dependent variables, respectively. In doing so, we investigated the influence of the factor GROUP on medium and upper alpha ratios as we expected that video gamers exhibit different event-related EEG alpha power modulations than NVGs. In addition to that, we investigated the influence of EXPOSURE DURATION and TIME ON TASK on medium and upper alpha ratios to control for modulations by different lengths of exposure durations (Klimesch et al., 2011) and time on task (Benwell et al., 2019). Afterward, we conducted two two-way ANOVAs with GROUP (NVGs vs. NAVGs vs. AVGs) as between-subjects factor, TIME ON TASK (Block 1 vs. Block 2) as within-subject factor and TVA C and K parameter values as dependent variables, respectively. We expected inter-individual differences in ERD in medium or upper alpha frequency bands between video gamers and NVGs to go along with inter-individual differences in TVA C parameter values, but not in K parameter values. However, if this was the case because EEG alpha power modulations and TVA C and K parameter values were associated, TVA C and K parameter values may also be modulated by time on task – and probably by different lengths of exposure durations. Therefore, we had to estimate TVA C and K parameter values for each block separately by estimating each participant’s TVA C and K parameter value based on their 210 experimental trials of each block – which is still a sufficient trial number to estimate reliable values (see Finke et al., 2005). However, we could not control for potential influences of exposure durations since TVA C and K parameter values are estimated based on accuracy data of all exposure durations, and hence it is not possible to compute them for one individual exposure duration (see above).

Finally, we conducted regression analyses with each participant’s TVA parameter difference value as criterion variable [see equation (3)], each participant’s alpha ratio difference value as predictor variable [see equation (4)], and GROUP as dummy variable (NVGs vs. NAVGs vs. AVGs) where NVGs were

used as reference to put the results of significant ANOVAs for alpha ratios and for TVA parameter values in relation to each other.

$$\begin{aligned} &TVA \text{ parameter difference value} \\ &= TVA \text{ parameter value}_{Block 2} \\ &\quad - TVA \text{ parameter value}_{Block 1} \end{aligned} \tag{3}$$

$$\begin{aligned} &alpha \text{ ratio difference value} \\ &= average \text{ alpha ratio}_{Block 2} \\ &\quad - average \text{ alpha ratio}_{Block 1} \end{aligned} \tag{4}$$

The regression model was built as described in equation (5), where Y indicates TVA parameter difference values, X alpha ratio difference values, i the index corresponding to a participant, α the intercept of the reference model (NVGs), β_1 the slope of the reference model, D_{ij} the dummy variable of group j , β_2 the difference in intercepts between NAVGs and NVGs, β_3 the difference in intercepts between AVGs and NVGs, β_4 the difference in slopes between NAVGs and NVGs, β_5 the difference in slopes between AVGs and NVGs and ϵ_i the residual term. We tested the significance of the whole model but not of the individual β_j parameter values. This is because β_j values may be potentially biased because of small group sample sizes yielding significant results without enough statistical power.

$$\begin{aligned} Y_i = &\alpha + \beta_1 X_i + \beta_2 D_{iNAVg} + \beta_3 D_{iAVg} + \beta_4 (X_i D_{iNAVg}) \\ &+ \beta_5 (X_i D_{iAVg}) + \epsilon_i \end{aligned} \tag{5}$$

RESULTS

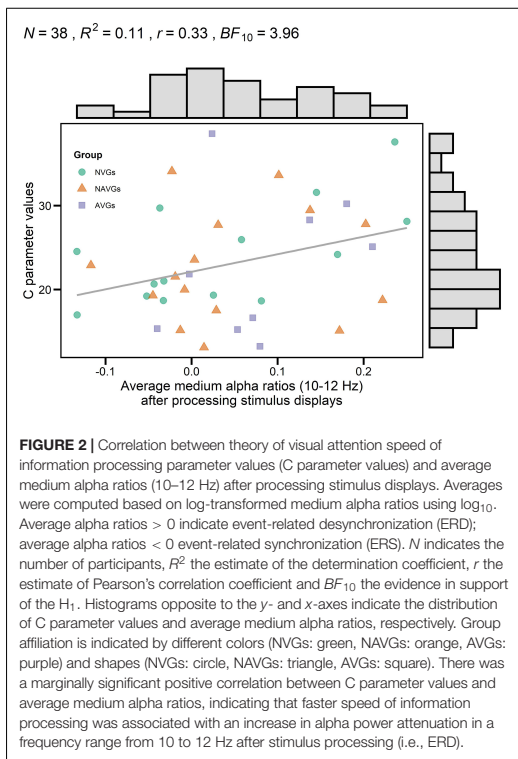
There was a marginally significant positive correlation between average medium alpha ratios and C parameter values, $R^2 = 0.11$, $r = 0.33$, $t(36) = 2.06$, $p_{uncorrected} = 0.023$, $p_{corrected} = 0.093$, $BF_{10} = 3.96$. But none of the other correlations reached significance (for a more detailed description, see Table 1). This correlation indicates that an increase in alpha power attenuation in a frequency band from 10 to 12 Hz after processing stimulus displays (i.e., ERD) goes along with an increase in speed of information processing. For a visualization of the association, see Figure 2.

However, as expected, the ANOVA with GROUP (NVGs vs. NAVGs vs. AVGs) as between-subjects factor, EXPOSURE

TABLE 1 | One-tailed Pearson’s moment correlation tests with average medium or average upper alpha ratios and theory of visual attention speed of information processing parameter values (C parameter values) or visual short-term memory capacity parameter values (K parameter values) as variables.

Model	<i>r</i>	<i>R</i> ²	<i>df</i>	<i>t</i>	<i>p</i>	<i>p</i> _{Bonferroni}	<i>BF</i> ₁₀
K parameter values and average medium alpha ratios	0.08	0.01	36	0.51	0.307	1.000	
K parameter values and average upper alpha ratios	0.20	0.04	36	1.23	0.114	0.454	
C parameter values and average medium alpha ratios	0.33	0.11	36	2.06	0.023	0.093	3.96
C parameter values and average upper alpha ratios	0.12	0.01	36	0.70	0.244	0.977	

r indicates Pearson’s correlation coefficients. *R*² indicates determination coefficients. *df* indicates degrees of freedom. *p* indicates uncorrected *p*-values. *p*_{Bonferroni} indicates *p*-values corrected by means of Bonferroni method. *BF*₁₀ indicates Bayes factors in favor of the *H*₁. *BF*₁₀ was only reported for (marginally) significant results after application of the Bonferroni method. Raw medium and upper alpha ratios were log-transformed using log₁₀ to prepare them for statistical analyses based on linear models.



DURATION (17.8, 35.6, 53.4, 89, 144.6, and 198 ms) and TIME ON TASK (Block 1 vs. Block 2) as within-subject factors and medium alpha ratios as dependent variable revealed a significant main effect EXPOSURE DURATION, $F(3.72, 130.37) = 16.80$, $p = 0.000$, $\eta_G^2 = 0.05$, $BF_{10} > 100$, indicating that the extent of alpha power attenuation in the frequency band from 10 to 12 Hz after stimulus processing was differentially modulated by exposure durations. Specifically, the extent of attenuation appeared to increase in relation to increasing exposure durations up to 144.6 ms, and to decrease with even longer exposure durations (for a visualization see Figure 3A). Hence, the correlation between average medium alpha ratios and C parameter values might be slightly contaminated by differential effects of exposure durations as medium alpha ratios were averaged without considering these intra-individual differences. Nevertheless, this procedure was inevitable as alpha ratios needed to be matched to the individual TVA C parameter values, respectively (see Computation of TVA C and K parameter values for a revision). A similar effect was found for upper alpha ratios, $F(3.63, 127.05) = 5.41$, $p = 0.001$, $\eta_G^2 = 0.02$, $BF_{10} > 100$ (see Figure 3B for a visualization).

But, more importantly, this ANOVA also revealed a significant interaction GROUP \times TIME ON TASK for medium alpha

ratios, $F(2, 35) = 4.80$, $p = 0.014$, $\eta_G^2 = 0.01$, $BF_{10} > 100$, suggesting that there were differential intra-individual differences in alpha power attenuation in the frequency band from 10 to 12 Hz between experimental blocks between video gamers and control participants. Specifically, participants exhibited larger medium alpha ratios – i.e., a stronger ERD – in Block 2 relative to Block 1, but AVGs showed the largest increase (see Figure 4A for a visualization). Thus, this result is partially in line with our hypotheses since we expected inter-individual differences in alpha oscillatory activity between video gamers and control participants and intra-individual differences between experimental blocks, but we did not expect the effects to interact with each other. None of the other main or interaction effects for medium or upper alpha ratios reached significance (see Tables 2, 3 for a more detailed inspection of the ANOVAs for medium or upper alpha ratios, respectively).

On top of that, the ANOVA with GROUP (NVGs vs. NAVGs vs. AVGs) as between-subjects factor and TIME ON TASK (Block 1 vs. Block 2) as within-subject factor for C parameter values revealed a significant interaction GROUP \times TIME ON TASK, $F(2, 35) = 3.99$, $p = 0.027$, $\eta_G^2 = 0.05$, $BF_{10} = 0.22$. This indicates that there were differential intra-individual differences in C parameter values between experimental blocks between video gamers and control participants. In detail, NVGs showed larger C values than video gamers in Block 1. In contrast, video gamers exhibited larger C values than NVGs in Block 2 with AVGs showing the largest increase (see Figure 4B). Thus, partially in line with our hypothesis, the temporal dynamics of TVA C parameter values were nicely paralleled by medium alpha ratios in video gamers but not in NVGs. None of the other main or interaction effects for C or K parameter values reached significance (for a detailed description of the ANOVAs for TVA C and K parameter values see Tables 4, 5, respectively).

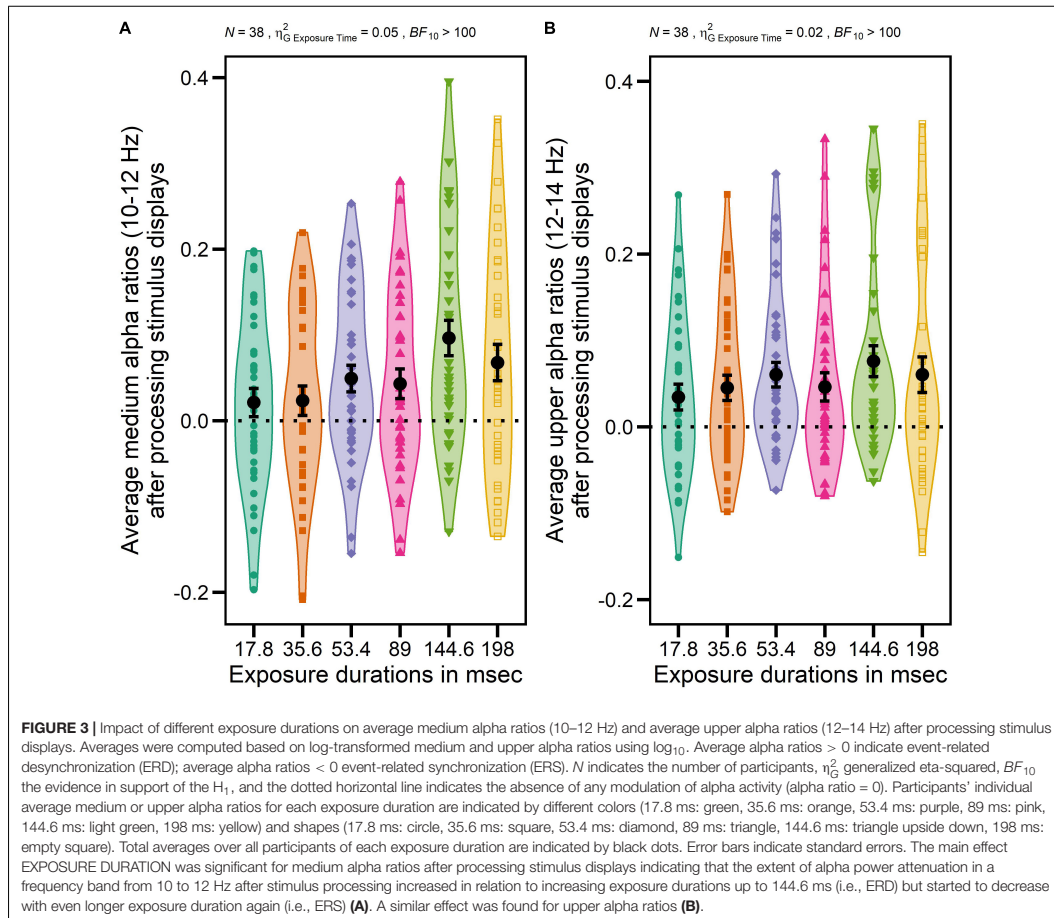
At last, we analyzed whether there was an association between the interaction effect for C and the interaction effect for medium alpha ratios by means of a regression analysis with C parameter difference values as criterion variable, medium alpha ratio difference values as predictor variable and GROUP as dummy variable (NVGs vs. NAVGs vs. AVGs) where NVGs were used as reference. One non-video gamer and one action video gamer had to be excluded from the analysis because they were identified as outliers. The regression analysis indicated that the model was significant, $R^2 = 0.41$, $F(5, 30) = 4.10$, $p = 0.006$, $BF_{10} = 8.29$. The estimated linear models for NVGs, NAVGs and AVGs can be inferred from equation (6), (7), and (8), respectively, where Y indicates C parameter difference values, X medium alpha ratio difference values, i the index corresponding to a participant and ϵ_i the residual term:

$$\text{NVGs} : Y_i = -1.64 - 34.22 * X_i + \epsilon_i \quad (6)$$

$$\text{NAVGs} : Y_i = 2.76 - 6.47 * X_i + \epsilon_i \quad (7)$$

$$\text{AVGs} : Y_i = -4.94 + 162.74 * X_i + \epsilon_i \quad (8)$$

By comparing the slope values between equations (6), (7), and (8), two differences between NVGs and NAVGs on the one side, and AVGs on the other side are observable: firstly,



in NVGs and NAVGs there seems to be a negative relation between C parameter difference values and medium alpha ratio difference values, indicating that if NAVGs and NVGs showed an increase in alpha power attenuation in a frequency band from 10 to 12 Hz in the second experimental block relative to the first one, their speed of information processing capacity might decrease. In contrast, in AVGs, there was a positive association, suggesting that if AVGs showed such an increase, their speed of information processing might increase. Secondly, the sizes of the slope values in NVGs and NAVGs were relatively smaller than those of AVGs. For a visualization of the linear models of each group, see Figure 5. This was in line with our previous results for NVGs and AVGs but not NAVGs – though one should not pay too much attention to the slope value of the NAVGs' model as it was quite small and hence not significant. Thus, our regression analysis seems to support our previous observation that intra-individual differences in alpha

power attenuation (10–12 Hz) and C parameter values between experimental blocks may be differentially associated depending on gaming behavior; and judging by the size of the slope value, this seems to apply especially to AVGs. However, these results should be considered with caution as the slope estimates in the AVGs model were heavily biased by a rather small sample of participants. For a more detailed description of the regression analysis, see Table 6.

DISCUSSION

Given that EEG alpha power modulations represent a neural substrate of attentional control, our results may support the idea that the conjunction between reward-related learning and attentional control represents a core mechanism in cognitive improvement in video gamers (Bavelier and Green, 2019). This

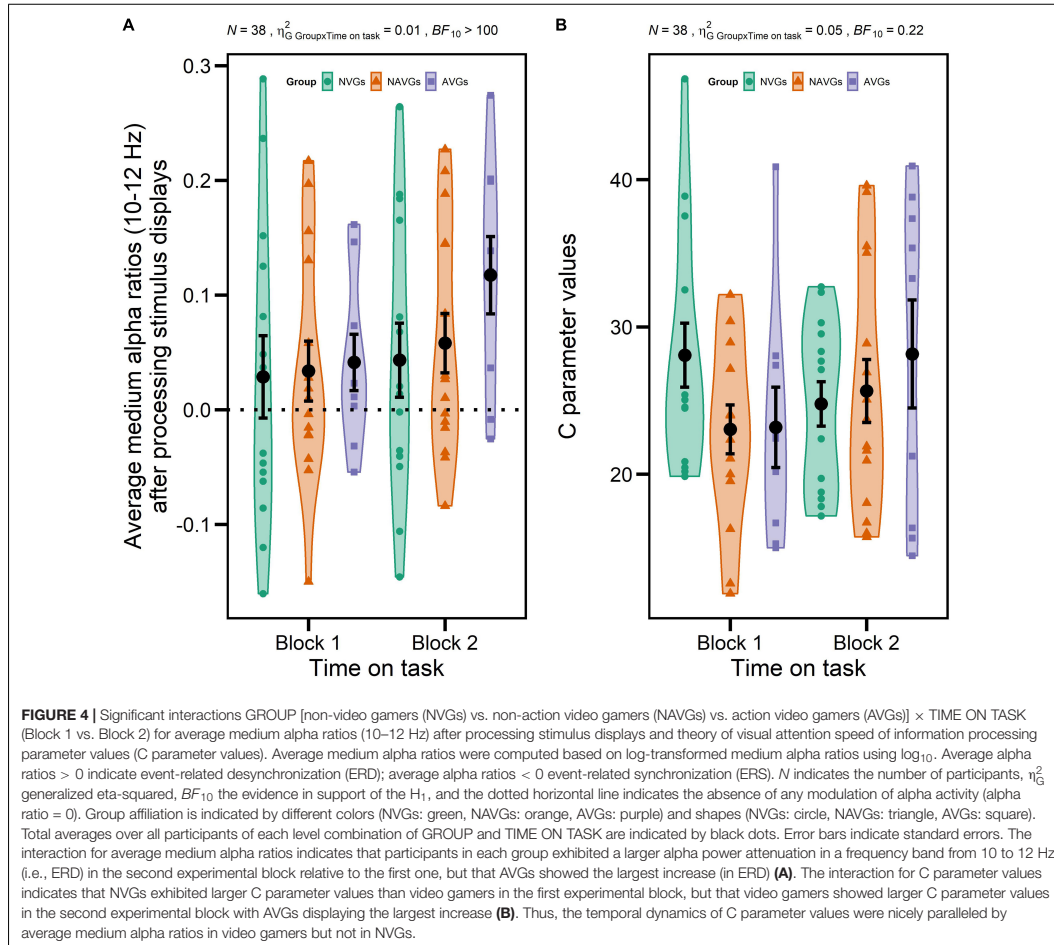


TABLE 2 | ANOVA with GROUP [non-video gamers (NVGs) vs. non-action video gamers (NAVGs) vs. action video gamers (AVGs)] as between-subjects factor, TIME ON TASK (Block 1 vs. Block 2) and EXPOSURE DURATION (17.8, 35.6, 53.4, 89, 144.6, and 198 ms) as within-subject factors and medium alpha ratios (10–12 Hz) as dependent variable.

Predictor	df_{Num}	df_{Den}	Epsilon	F	p	η^2_G	BF_{10}
Group	2.00	35.00		0.47	0.626	0.02	
Time on task	1.00	35.00		17.65	0.000	0.02	>100
Group × Time on task	2.00	35.00		4.80	0.014	0.01	>100
Exposure duration	3.72	130.37	0.74	16.80	0.000	0.05	>100
Group × Exposure duration	7.45	130.37	0.74	0.90	0.510	0.01	
Time on task × Exposure duration	4.14	144.77	0.83	0.61	0.662	0.00	
Group × Time on task × Exposure duration	8.27	144.77	0.83	0.64	0.749	0.00	

df_{Num} indicates degrees of freedom numerator. df_{Den} indicates degrees of freedom denominator. Epsilon indicates Greenhouse–Geisser multiplier for degrees of freedom, p-values and degrees of freedom in the table incorporate this correction. η^2_G indicates generalized eta-squared. BF_{10} indicates Bayes factors in favor of the H_1 . BF_{10} was only reported for significant main or interaction effects. Raw medium alpha ratios were log-transformed using \log_{10} to prepare them for statistical analyses based on linear models.

TABLE 3 | ANOVA with GROUP [non-video gamers (NVGs) vs. non-action video gamers (NAVGS) vs. action video gamers (AVGs)] as between-subjects factor, TIME ON TASK (Block 1 vs. Block 2) and EXPOSURE DURATION (17.8, 35.6, 53.4, 89, 144.6, and 198 ms) as within-subject factors and upper alpha ratios (12–14 Hz) as dependent variable.

Predictor	df _{Num}	df _{Den}	Epsilon	F	p	η^2_G	BF ₁₀
Group	2.00	35.00		2.69	0.082	0.11	
Time on task	1.00	35.00		2.27	0.141	0.00	
Group × Time on task	2.00	35.00		0.67	0.516	0.00	
Exposure duration	3.63	127.05	0.73	5.41	0.001	0.02	> 100
Group × Exposure duration	7.26	127.05	0.73	0.96	0.467	0.01	
Time on task × Exposure duration	4.59	160.63	0.92	0.77	0.564	0.00	
Group × Time on task × Exposure duration	9.18	160.63	0.92	1.17	0.315	0.00	

df_{Num} indicates degrees of freedom numerator. df_{Den} indicates degrees of freedom denominator. Epsilon indicates Greenhouse–Geisser multiplier for degrees of freedom, p-values and degrees of freedom in the table incorporate this correction. η^2_G indicates generalized eta-squared. BF₁₀ indicates Bayes factors in favor of the H₁. BF₁₀ was only reported for significant main or interaction effects. Raw upper alpha ratios were log-transformed using log₁₀ to prepare them for statistical analyses based on linear models.

TABLE 4 | ANOVA with GROUP [non-video gamers (NVGs) vs. non-action video gamers (NAVGS) vs. action video gamers (AVGs)] as between-subjects factor, TIME ON TASK (Block 1 vs. Block 2) as within-subject factor and theory of visual attention speed of information processing parameter values (C parameter values) as dependent variable.

Predictor	df _{Num}	df _{Den}	F	p	η^2_G	BF ₁₀
Group	2	35	0.33	0.720	0.01	
Time on task	1	35	0.67	0.418	0.00	
Group × Time on task	2	35	3.99	0.027	0.05	0.22

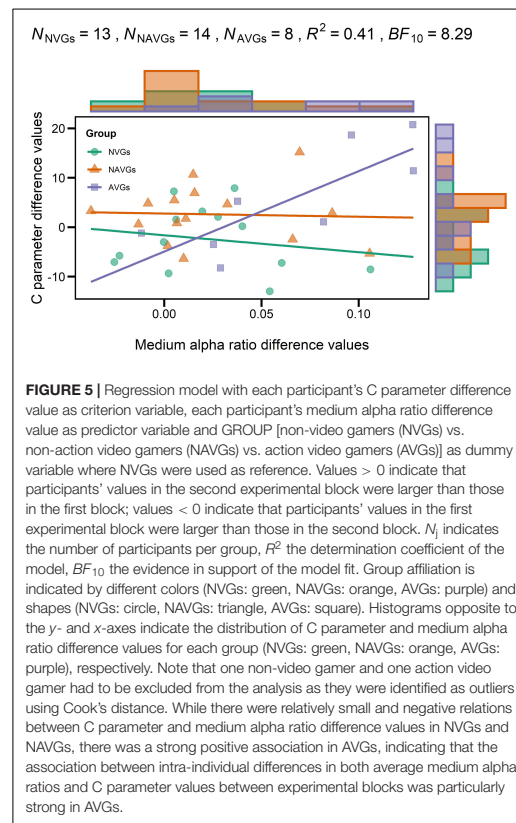
df_{Num} indicates degrees of freedom numerator. df_{Den} indicates degrees of freedom denominator. η^2_G indicates generalized eta-squared. BF₁₀ indicates Bayes factors in favor of the H₁. BF₁₀ was only reported for significant main or interaction effects. Note that the low BF₁₀ value for the GROUP × TIME ON TASK interaction was to be expected as neither the main effect GROUP nor the main effect TIME ON TASK were significant.

TABLE 5 | ANOVA with GROUP [non-video gamers (NVGs) vs. non-action video gamers (NAVGS) vs. action video gamers (AVGs)] as between-subjects factor, TIME ON TASK (Block 1 vs. Block 2) as within-subject factor and theory of visual attention short-term memory capacity parameter values (K parameter values) as dependent variable.

Predictor	df _{Num}	df _{Den}	F	p	η^2_G
Group	2	35	0.94	0.400	0.04
Time on task	1	35	0.16	0.694	0.00
Group × Time on task	2	35	1.82	0.178	0.01

df_{Num} indicates degrees of freedom numerator. df_{Den} indicates degrees of freedom denominator. η^2_G indicates generalized eta-squared.

is because, we found that inter-individual differences in speed of information processing as operationalized by TVA between video gamers and NVGs were associated with inter-individual differences in post-stimulus EEG alpha power attenuation from 10 to 12 Hz. Hereby, it was particularly interesting that video gamers did not outperform NVGs right from the start but in the course of performing the paradigm and that this was paralleled by an increase in alpha ERD in video gamers but not in NVGs – which is well in line with the learning to learn approach (Bavelier et al., 2012b; Green and Bavelier, 2012). Moreover, it was quite interesting that our regression analysis indicated that foremost



AVGs might benefit from this increase in alpha ERD as they showed the strongest positive relation between TVA C parameter and medium alpha ratio difference values – which supports the idea that gamers might benefit specifically from playing

TABLE 6 | Regression analysis with C parameter difference values as criterion variable, medium alpha ratio difference values as predictor variable and GROUP as dummy variable [non-video gamers (NVGs) vs. non-action video gamers (NAVGS) vs. action video gamers (AVGs)] where NVGs were used as reference.

Predictor	b	b 95% CI [LL, UL]	Fit
Intercept	-1.64	[-6.09, 2.81]	
Medium alpha ratio difference values	-34.22	[-139.63, 71.18]	
NAVGS	4.40	[-1.62, 10.41]	
AVGS	-3.30	[-12.28, 5.68]	
Medium alpha ratio difference values × NAVGS	27.76	[-109.95, 165.47]	
Medium alpha ratio difference values × AVGS	196.96	[53.72, 340.20]	
			$R^2 = 0.41$ 95% CI[0.05, 0.53] $F(5, 30) = 4.10,$ $p = 0.006,$ $BF_{10} = 8.29$

b represents unstandardized regression weights. LL and UL indicate the lower and upper limits of a confidence interval without corrections for multiple comparisons, respectively. R^2 indicates the determination coefficient. BF_{10} indicates the Bayes factor in favor of the model fit.

action video games (Achtman et al., 2008). Therefore, our data suggest that attentional control as operationalized by EEG alpha power modulations might play a considerable role in learning mechanisms relevant for cognitive improvement in video gamers (Bavelier and Green, 2019).

We show that alpha ERD in a frequency range from 10 to 12 Hz may represent a neural substrate of speed of information processing as operationalized by TVA. Considering that the extent of ERD in a similar alpha frequency band after stimulus processing had already been related to reaction times (Nenert et al., 2012), this result was not surprising, but it might play a considerable role for new vistas on TVA. This is because, according to TVA (Bundesen, 1990; Kyllingsbaek, 2006; Dyrholm et al., 2011; Bundesen et al., 2015), visual information is processed by means of two core attentional processing components, i.e., filtering and pigeonholing, where filtering allows the selection of specific visual features, e.g., colors, while pigeonholing allows for the selection of visual categories, e.g., letters (Broadbent, 1970). Based on the assumption that all visual information is processed in parallel and that there is a limited capacity of the visual short-term memory store, filtering and pigeonholing represent mechanisms to determine the processing rate or probability for a visual stimulus to be encoded into the visual short-term memory store as described by the rate equation (9)

$$v_x(i) = \eta(x, i)\beta_i \frac{w_x}{\sum_{z \in S} w_z} \tag{9}$$

where $v_x(i)$ indicates the processing rate that x is an element of category i , $\eta(x, i)$ the sensory evidence that x is an element of i , β_i the perceptual decision bias to favor category i over other categories, and w_x the relative attentional weight in favor of an object x – which is divided by the sum of attentional weights of

all remaining objects in the visual field S . The attentional weight term w_x can be described further by equation (10)

$$w_x = \sum_{j \in G} \eta(x, j)\pi_j \tag{10}$$

where j indicates a visual category aka visual feature, G the set of all features that may be associated with a pertinence value, $\eta(x, j)$ the sensory evidence that x belongs to feature j , and π_j the pertinence or weight in favor of a feature j (Dyrholm et al., 2011). Thus, β_i and w_x represent pigeonholing and filtering, respectively. On top of that, based on the assumption that the rate equation is dependent on the exposure duration of visual stimuli and the number of visual stimuli in the visual field, and that the attentional capacities of healthy humans are equally spread across the visual field, $v_x(i)$ may also be considered as a fraction of the total processing capacity at a given time point in a multi-stimulus setting where the processing capacity is spread across the whole visual field. Thus, the processing rate of a stimulus can also be described according to equation (11)

$$v_x = C \frac{w_x}{\sum_{z \in S} w_z} \tag{11}$$

where v_x indicates the processing rate of an object x , C the fixed limited processing capacity measured in Hz or the number of elements that can be encoded per second (aka TVA's speed of information processing parameter) and w_x the relative attentional weight in favor of object x (Dyrholm et al., 2011). Thus, according to TVA, visual speed of information processing is moderated by the attentional weighting term – or by an individual's filtering capacity.

Based on Klimesch (1997, 2012) and Klimesch et al. (2011), one might expect that oscillatory activity in the lower alpha frequency band was associated with TVA's rate equation. But in contrast, our data suggest that higher-level cognitive processing might be a mechanism either of the C parameter or the conjunction between the C and the attentional weight parameters as C parameter values were associated with alpha power attenuation in a frequency band from 10 to 12 Hz after stimulus processing. A potential explanation here might be that the two parameters may represent the retrieval of specific *knowledge systems* to semantically encode sensory information (Klimesch et al., 2011; Klimesch, 2012). According to Klimesch et al. (2011) and Klimesch (2012), a knowledge system refers to a neural network that is associated with implicit and explicit aspects of long-term memory. Hereby, alpha phase alignments in the medium or upper alpha frequency bands are assumed to represent the onset of retrieving from a knowledge system, while alpha power modulations in the medium or upper alpha frequency band may modulate the amplification of the retrieval of relevant and the suppression of the retrieval of irrelevant information from a knowledge system (Klimesch et al., 2011; Klimesch, 2012). But further research investigating the role of lower alpha oscillations and the conjunction between lower and medium or upper alpha oscillations and TVA C as well as w_x parameter values would be necessary to gain more insights on the role of knowledge systems in TVA.

Furthermore, we would like to discuss potential implications of our results at the intersection of computer sciences, health care and the gaming industry. Considering that there are already customized video games that are used for clinical purposes (Kollins et al., 2020); and video games where on-screen characters may even be controlled by means of brain oscillatory activity or event-related potentials using brain-computer interfaces (Bayliss, 2003; Nijholt et al., 2009), which may enable people with a physical disability to enjoy video gaming and feel more inclusive (see, Bos et al., 2010, for a more detailed review), one might question the significance of gaming effects associated with commercially available video games. One of the largest shortcomings of the latter is the lack of standardization. The issue here is that if we compare markers of neural activity and cognitive processing between participants who differ in their gaming behavior, or even if we compare changes in such markers associated with video gaming training regimes, we can hardly tell what differential characteristics between the groups or between the training regimes caused the inter-individual differences in neural activity and cognitive processing. On the other hand, research on gaming effects related to commercially available video games lays the foundation for the development of customized video games for clinical treatment, for fostering learning abilities, or for making commercially available video games even more entertaining. This is because, these frequent observations that inter-individual differences in neural and cognitive processing may be related to inter-individual differences in gaming behavior tell us that there may be aspects of commercially available video games that play a considerable role for human learning. Understanding the mechanisms underlying these phenomena, in turn, may then be the key for more significant or fruitful applications. For instance, if EEG alpha power modulations specifically in the medium and upper frequency bands turn out to be a robust neural substrate of cognitive improvements associated with playing commercially available video games, they could be used as a parameter for adjusting the complexity of the gameplay of video games in brain-computer interfaces.

With this being said, we would like to discuss some of the shortcomings in our experimental design as well. For instance, our individual group samples sizes were rather small which indicates a low statistical power. But considering that most of our statistical analyses (Pearson's moment correlation tests, ANOVAs and regression analysis) were based on our total sample size (outliers not included), our statistical power should be acceptable. On top of that, we used type II sums of squares to compensate for unbalanced group samples (Langsrud, 2003); and in addition to that, our samples were similar to sample sizes of previous research on gaming effects (Li et al., 2009, 2011; Wu et al., 2012; Wilms et al., 2013; Schubert et al., 2015). Thus, we acknowledge that statistical power might be considered an issue in our study, but we argue that we used statistical methods that were less prone to individual group sample sizes and therefore, sufficient to identify reliable gaming effects. Furthermore, we did not find correlations between K parameter values and alpha ratios. We suggest that a reason for this may be that we analyzed a rather early time window where the CDA may not yet have been fully observable:

Wiegand et al. (2014b), for instance, observed the onset of this event-related potential approximately 300 ms after stimulus processing and it persisted until a response was provided. By combining TVA data and EEG data from two different paradigms where no mask displays were used in the EEG paradigm but a blank screen of 900 ms, it was possible to investigate the CDA (Wiegand et al., 2014a,b, 2016). In contrast, based on our experimental design, it was more difficult to study this time window as we used mask displays and ratios based on 500 ms segments.

Besides, we did not exactly replicate previous findings where video gamers exhibited larger C parameter values than NVGs (Wilms et al., 2013; Schubert et al., 2015). We believe that one plausible reason for this might be that we used different classification criteria for participants than Wilms et al. (2013) and Schubert et al. (2015). Wilms et al. (2013), for instance, classified participants as experienced players if they had played action video games for more than 15 h a month, as casual players if they had played 4–8 h per month and as non-players if they played less than 2 h per months. In contrast, Schubert et al. (2015) classified participants as video game experts if they had played action video games at least 10 h a week in the last 6–12 months or as non-experts if they had played action video games less than 1 h a week in the last 6–12 months. In comparison, we also considered additional gaming habits to action video gaming, and we used different time constraints (Green et al., 2017). Thus, and in consideration that the classification of participants according to their gaming behavior may be in any case somehow arbitrary given that, for instance, action video games can be understood as video games where “under the most basic definition the player's on-screen character can run, jump, roll, shoot, or fly, but the defining characteristic is that enemies and obstacles are overcome by physical means, rather than involved intellectual problem solving” (Next Generation, 1996, p. 29) (which is a rather unspecific description), we argue that differences in classification criteria are likely associated with slightly different gaming effects. Recruiting more specified and, hence, more differentiable groups might be a solution for this. For instance, Qiu et al. (2018) subdivided participants in AVGs and control participants based on their reported skill score in the video game League of Legends. Alternatively, in an attempt to increase effects between groups, a gaming group of professional e-sportsmen/sportswomen could be recruited.

Another limitation might be that despite our efforts to properly process the data, either our EEG power values, or our TVA estimates might not have been perfectly accurate because e.g., the factor exposure duration might have contaminated our procedures. Such contaminations are, unfortunately, inevitable using TVA-algorithms. Moreover, we need to point out that our data only show a correlational and not a causal relation between faster visual information processing and EEG alpha power modulations in gamers. To show a causal relation, one might need to apply an experimental design comprising a video gaming training regime.

Nevertheless, our data indicate that there may be inter-individual differences in event-related EEG alpha power

modulations related to inter-individual differences in habitual gaming behavior, and that these modulations might go along with inter-individual differences in speed of visual information processing as operationalized by TVA. We conclude from this, that EEG alpha power modulations may be a promising neural substrate of alterations in visual cognitive processing in video gamers.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the local ethics review board. The

patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

YH contributed to the conceptualization, data curation, formal analysis, investigation, methodology, project administration, and software development of this study. JM contributed significantly to the software development. JF contributed to the conceptualization and validation of this study. PS contributed to the conceptualization, funding acquisition, resources, and validation of this study. All the authors contributed to the article and approved the submitted version.

FUNDING

This work was supported by Deutsche Forschungsgemeinschaft (Grant Number SA 1872/2-2).

REFERENCES

- Abdi, H. (2010). "The greenhouse-geisser correction," in *Encyclopedia of Research Design*, ed. N. Salkind (Thousand Oaks, CA: Sage), 544–548.
- Achtman, R. L., Green, C. S., and Bavelier, D. (2008). Video games as a tool to train visual skills. *Restor. Neurol. Neurosci.* 26, 435–446.
- Bavelier, D., Achtman, R. L., Mani, M., and Föcker, J. (2012a). Neural bases of selective attention in action video game players. *Vis. Res.* 61, 132–143. doi: 10.1016/j.visres.2011.08.007
- Bavelier, D., Green, C. S., Pouget, A., and Schrater, P. (2012b). Brain plasticity through the life span: learning to learn and action video games. *Annu. Rev. Neurosci.* 35, 391–416. doi: 10.1146/annurev-neuro-060909-152832
- Bavelier, D., and Green, C. S. (2019). Enhancing attentional control: lessons from action video games. *Neuron* 104, 147–163. doi: 10.1016/j.neuron.2019.09.031
- Bayliss, J. D. (2003). Use of the evoked potential P3 component for control in a virtual apartment. *IEEE Trans. Neural. Syst. Rehabil. Eng.* 11, 113–116. doi: 10.1109/TNSRE.2003.814438
- Bediou, B., Adams, D. M., Mayer, R. E., Tipton, E., Green, C. S., and Bavelier, D. (2018). Meta-analysis of action video game impact on perceptual, attentional, and cognitive skills. *Psychol. Bull.* 144, 77–110. doi: 10.1037/bul0000130
- Bejjanki, V. R., Zhang, R., Li, R., Pouget, A., Green, C. S., Lu, Z.-L., et al. (2014). Action video game play facilitates the development of better perceptual templates. *Proc. Natl. Acad. Sci. U.S.A.* 111, 16961–16966. doi: 10.1073/pnas.1417056111
- Benwell, C. S. Y., London, R. E., Tagliabue, C. F., Veniero, D., Gross, J., Keitel, C., et al. (2019). Frequency and power of human alpha oscillations drift systematically with time-on-task. *NeuroImage* 192, 101–114. doi: 10.1016/j.neuroimage.2019.02.067
- Blackler, K. J., and Curby, K. M. (2013). Enhanced visual short-term memory in action video game players. *Atten. Percept. Psychophys.* 75, 1128–1136. doi: 10.3758/s13414-013-0487-0
- Blackler, K. J., Curby, K. M., Klobusicky, E., and Chein, J. M. (2014). Effects of action video game training on visual working memory. *J. Exp. Psychol. Hum. Percept. Perform.* 40, 1992–2004. doi: 10.1037/a0037556
- Bland, J. M., and Altman, D. G. (1995). Multiple significance tests: the Bonferroni method. *BMJ* 310:170. doi: 10.1136/bmj.310.6973.170
- Boot, W. R., Blakely, D. P., and Simons, D. J. (2011). Do action video games improve perception and cognition? *Front. Psychol.* 2:226. doi: 10.3389/fpsyg.2011.00226
- Bos, D. P.-O., Reuderink, B., van der Laar, B., Gürkök, H., Mühl, C., Poel, M., et al. (2010). "Brain-computer interfacing and Games," in *Brain-Computer Interfaces*, eds D. S. Tan and A. Nijholt (London: Springer-Verlag), 149–178. doi: 10.1007/978-1-84996-272-8_10
- Broadbent, D. E. (1970). "Stimulus set and response set: two kinds of selective attention," in *Attention: Contemporary Theory and Analysis*, ed. D. Mostofsky (New York, NY: Appleton-Century Crofts), 51–60.
- Bundesen, C. (1990). A theory of visual attention. *Psychol. Rev.* 97, 523–547. doi: 10.1037/0033-295X.97.4.523
- Bundesen, C., Vangkilde, S., and Petersen, A. (2015). Recent developments in a computational theory of visual attention (TVA). *Vis. Res.* 116, 210–218. doi: 10.1016/j.visres.2014.11.005
- Cain, M. S., Landau, A. N., and Shimamura, A. P. (2012). Action video game experience reduces the cost of switching tasks. *Atten. Percept. Psychophys.* 74, 641–647. doi: 10.3758/s13414-012-0284-1
- Cain, M. S., Prinzmetal, W., Shimamura, A. P., and Landau, A. N. (2014). Improved control of exogenous attention in action video game players. *Front. Psychol.* 5:69. doi: 10.3389/fpsyg.2014.00069
- Capotosto, P., Babiloni, C., Romani, G. L., and Corbetta, M. (2009). Frontoparietal cortex controls spatial attention through modulation of anticipatory alpha rhythms. *J. Neurosci.* 29, 5863–5872. doi: 10.1523/JNEUROSCI.0539-09.2009
- Chisholm, J. D., and Kingstone, A. (2012). Improved top-down control reduces oculomotor capture: the case of action video game players. *Atten. Percept. Psychophys.* 74, 257–262. doi: 10.3758/s13414-011-0253-0
- Chun, M. M., Golomb, J. D., and Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annu. Rev. Psychol.* 62, 73–101. doi: 10.1146/annurev.psych.093008.100427
- Colzato, L. S., van Leeuwen, P. J. A., van den Wildenberg, W. P. M., and Hommel, B. (2010). DOOM'd to SWITCH: superior cognitive flexibility in players of first person shooter games. *Front. Psychol.* 1:8. doi: 10.3389/fpsyg.2010.00008
- Cook, R. D. (1977). Detection of influential observation in linear regression. *Technometrics* 19, 15–18. doi: 10.2307/1268249
- Corbetta, M., Patel, G., and Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324. doi: 10.1016/j.neuron.2008.04.017
- Deroy, O., Spence, C., and Noppeney, U. (2016). Metacognition in multisensory perception. *Trends Cogn. Sci.* 20, 736–747. doi: 10.1016/j.tics.2016.08.006
- Dye, M. W. G., Green, C. S., and Bavelier, D. (2009). Increasing speed of processing with action video games. *Curr. Dir. Psychol. Sci.* 18, 321–326. doi: 10.1111/j.1467-8721.2009.01660.x
- Dyrholm, M., Kyllingsbæk, S., Espeseth, T., and Bundesen, C. (2011). Generalizing parametric models by introducing trial-by-trial parameter variability: the case of TVA. *J. Math. Psychol.* 55, 416–429. doi: 10.1016/j.jmp.2011.08.005

- Entertainment Software Association (2019). *2019 Essential Facts About the Computer and Video Game Industry*. Available at: <https://www.theesa.com/esa-research/2019-essential-facts-about-the-computer-and-video-game-industry/>.
- Finke, K., Bublak, P., Krummenacher, J., Kyllingsbaek, S., Muller, H. J., and Schneider, W. X. (2005). Usability of a theory of visual attention (TVA) for parameter-based measurement of attention I: evidence from normal subjects. *J. Inter. Neuropsych. Soc.* 11, 832–842. doi: 10.1017/s1355617705050976
- Föcker, J., Cole, D., Beer, A. L., and Bavelier, D. (2018). Neural bases of enhanced attentional control: lessons from action video game players. *Brain Behav.* 8:e01019. doi: 10.1002/brb3.1019
- Föcker, J., Mortazavi, M., Khoe, W., Hillyard, S. A., and Bavelier, D. (2019). Neural correlates of enhanced visual attentional control in action video game players: an event-related potential study. *J. Cogn. Neurosci.* 31, 377–389. doi: 10.1162/jocn_a_01230
- Freunberger, R., Klimesch, W., Griesmayr, B., Sauseng, P., and Gruber, W. (2008). Alpha phase coupling reflects object recognition. *NeuroImage* 42, 928–935. doi: 10.1016/j.neuroimage.2008.05.020
- Fries, P. (2015). Rhythms for cognition: communication through coherence. *Neuron* 88, 220–235. doi: 10.1016/j.neuron.2015.09.034
- Gambacorta, C., Nahum, M., Vedamurthy, L., Bayliss, J., Jordan, J., Bavelier, D., et al. (2018). An action video game for the treatment of amblyopia in children: a feasibility study. *Vis. Res.* 148, 1–14. doi: 10.1016/j.visres.2018.04.005
- Green, C. S., and Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature* 423, 534–537. doi: 10.1038/nature01647
- Green, C. S., and Bavelier, D. (2007). Action-video-game experience alters the spatial resolution of vision. *Psychol. Sci.* 18, 88–94. doi: 10.1111/j.1467-9280.2007.01853.x
- Green, C. S., and Bavelier, D. (2012). Learning, attentional control, and action video games. *Curr. Biol.* 22, R197–R206. doi: 10.1016/j.cub.2012.02.012
- Green, C. S., Kattner, F., Eichenbaum, A., Bediou, B., Adams, D. M., Mayer, R. E., et al. (2017). Playing some video games but not others is related to cognitive abilities: a critique of Unsworth et al. (2015). *Psychol. Sci.* 28, 679–682. doi: 10.1177/0956797616644837
- Green, C. S., Pouget, A., and Bavelier, D. (2010). Improved probabilistic inference as a general learning mechanism with action video games. *Curr. Biol.* 20, 1573–1579. doi: 10.1016/j.cub.2010.07.040
- Green, C. S., Sugarman, M. A., Medford, K., Klobusicky, E., and Bavelier, D. (2012). The effect of action video game experience on task-switching. *Comput. Hum. Behav.* 28, 984–994. doi: 10.1016/j.chb.2011.12.020
- Greenfield, P. M., DeWinstanley, P., Kilpatrick, H., and Kaye, D. (1994). Action video games and informal education: effects on strategies for dividing visual attention. *J. Appl. Dev. Psychol.* 15, 105–123. doi: 10.1016/0193-3973(94)90008-6
- Gruber, W. R., Klimesch, W., Sauseng, P., and Doppelmayr, M. (2005). Alpha phase synchronization predicts P1 and N1 latency and amplitude size. *Cereb. Cortex* 15, 371–377. doi: 10.1093/cercor/bhh139
- Hanslmayr, S., Spitzer, B., and Bäuml, K.-H. (2009). Brain oscillations dissociate between semantic and nonsemantic encoding of episodic memories. *Cereb. Cortex* 19, 1631–1640. doi: 10.1093/cercor/bhn197
- Hazarika, J., and Dasgupta, R. (2020). Neural correlates of action video game experience in a visuospatial working memory task. *Neural Comput. Appl.* 32, 3431–3440. doi: 10.1007/s00521-018-3713-9
- Hazarika, J., Kant, P., Dasgupta, R., and Laskar, S. H. (2018). Neural modulation in action video game players during inhibitory control function: an EEG study using discrete wavelet transform. *Bioméd. Signal Process. Control* 45, 144–150. doi: 10.1016/j.bspc.2018.05.023
- Jensen, O., and Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.* 4:186. doi: 10.3389/fnhum.2010.00186
- Kassambara, A. (2020). *rstatix: Pipe-Friendly Framework for Basic Statistical Tests*. R Package Version 0.6.0. Available at: <https://CRAN.R-project.org/package=rstatix> (accessed June 18, 2020).
- Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *Int. J. Psychophysiol.* 26, 319–340. doi: 10.1016/S0167-8760(97)00773-3
- Klimesch, W. (2012). α -band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* 16, 606–617. doi: 10.1016/j.tics.2012.10.007
- Klimesch, W., Fellinger, R., and Freunberger, R. (2011). Alpha oscillations and early stages of visual encoding. *Front. Psychol.* 2:118. doi: 10.3389/fpsyg.2011.00118
- Klimesch, W., Hanslmayr, S., Sauseng, P., Gruber, W. R., and Doppelmayr, M. (2007a). P1 and traveling alpha waves: evidence for evoked oscillations. *J. Neurophysiol.* 97, 1311–1318. doi: 10.1152/jn.00876.2006
- Klimesch, W., Sauseng, P., and Hanslmayr, S. (2007b). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res. Rev.* 53, 63–88. doi: 10.1016/j.brainresrev.2006.06.003
- Klimesch, W., Schack, B., Schabus, M., Doppelmayr, M., Gruber, W., and Sauseng, P. (2004). Phase-locked alpha and theta oscillations generate the P1-N1 complex and are related to memory performance. *Brain Res. Cogn. Brain Res.* 19, 302–316. doi: 10.1016/j.cogbrainres.2003.11.016
- Koepp, M. J., Gunn, R. N., Lawrence, A. D., Cunningham, V. J., Dagher, A., Jones, T., et al. (1998). Evidence for striatal dopamine release during a video game. *Nature* 393, 266–268. doi: 10.1038/30498
- Kollins, S. H., DeLoss, D. J., Cañadas, E., Lutz, J., Findling, R. L., Keefe, R. S. E., et al. (2020). A novel digital intervention for actively reducing severity of paediatric ADHD (STARS-ADHD): a randomised controlled trial. *Lancet Digital Health* 2, e168–e178. doi: 10.1016/S2589-7500(20)30017-0
- Krishnan, L., Kang, A., Sperling, G., and Srinivasan, R. (2013). Neural strategies for selective attention distinguish fast-action video game players. *Brain Topogr.* 26, 83–97. doi: 10.1007/s10548-012-0232-3
- Kühn, S., Romanowski, A., Schilling, C., Lorenz, R., Mörsen, C., Seifert, N., et al. (2011). The neural basis of video gaming. *Transl. Psychiatry* 1:e53. doi: 10.1038/tp.2011.53
- Kyllingsbaek, S. (2006). Modeling visual attention. *Behav. Res. Methods* 38, 123–133. doi: 10.3758/bf03192757
- Langsrud, Ø (2003). ANOVA for unbalanced data: use type ii instead of type iii sums of squares. *Stat. Comput.* 13, 163–167. doi: 10.1023/A:1023260610025
- Lawrence, M. A. (2016). *ez: Easy analysis and Visualization of Factorial Experiments*. R Package Version 4.4-0. Available at: <https://CRAN.R-project.org/package=ez> (accessed November 02, 2016).
- Levene, H. (1960). “Robust tests for equality of variances,” in *Contributions to Probability and Statistics: Essays in Honor of Harold Hotelling*, eds I. Olkin and H. Hotelling (Palo Alto, CA: Stanford University Press), 278–292.
- Li, R., Polat, U., Makous, W., and Bavelier, D. (2009). Enhancing the contrast sensitivity function through action video game training. *Nat. Neurosci.* 12, 549–551. doi: 10.1038/nn.2296
- Li, R., Polat, U., Scalzo, F., and Bavelier, D. (2010). Reducing backward masking through action game training. *J. Vis.* 10:33. doi: 10.1167/10.14.33
- Li, R. W., Ngo, C., Nguyen, J., and Levi, D. M. (2011). Video-game play induces plasticity in the visual system of adults with amblyopia. *PLoS Biol.* 9:e1001135. doi: 10.1371/journal.pbio.1001135
- Lüdtke, D., Makowski, D., Waggoner, P., and Patil, I. (2020). *performance: Assessment of Regression Models Performance*. R Package Version 0.4.7. Available at: <https://CRAN.R-project.org/package=performance> (accessed June 14, 2020).
- McDermott, A. F., Bavelier, D., and Green, C. S. (2014). Memory abilities in action video game players. *Comput. Hum. Behav.* 34, 69–78. doi: 10.1016/j.chb.2014.01.018
- Mishra, J., Zinni, M., Bavelier, D., and Hillyard, S. A. (2011). Neural basis of superior performance of action videogame players in an attention-demanding task. *J. Neurosci.* 31, 992–998. doi: 10.1523/JNEUROSCI.4834-10.2011
- Moray, R. D., and Roudier, J. N. (2018). *BayesFactor: Computation of Bayes Factors for Common Designs*. R Package Version 0.9.12-4.2. (accessed May, 19, 2018).
- Nenert, R., Viswanathan, S., Dubuc, D. M., and Visscher, K. M. (2012). Modulations of ongoing alpha oscillations predict successful short-term visual memory encoding. *Front. Hum. Neurosci.* 6:127. doi: 10.3389/fnhum.2012.00127
- Neuwirth, E. (2014). *RColorBrewer: ColorBrewer Palettes*. R Package Version 1.1-2. Available at: <https://CRAN.R-project.org/package=RColorBrewer> (accessed December 07, 2014).
- Next Generation (1996). *The Next Generation Lexicon A To Z: A Definitive Guide To Gaming Terminology*. Available at: <https://archive.org/details/nextgen-issue-015/page/n29/mode/2up>.
- Nijholt, A., Bos, D. P. O., and Reuderink, B. (2009). Turning shortcomings into challenges: brain–computer interfaces for games. *Entertain. Comput.* 1, 85–94. doi: 10.1016/j.entcom.2009.09.007

- Nobre, A. C., and van Ede, F. (2018). Anticipated moments: temporal structure in attention. *Nat. Rev. Neurosci.* 19, 34–48. doi: 10.1038/nrn.2017.141
- Olejnik, S., and Algina, J. (2003). Generalized eta and omega squared statistics: measures of effect size for some common research designs. *Psychol. Methods* 8, 434–447. doi: 10.1037/1082-989X.8.4.434
- Pavan, A., Hobaek, M., Blurton, S. P., Contillo, A., Ghin, F., and Greenlee, M. W. (2019). Visual short-term memory for coherent motion in video game players: evidence from a memory- masking paradigm. *Sci. Rep.* 9:6027. doi: 10.1038/s41598-019-42593-0
- Pfurtscheller, G., and Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin. Neurophysiol.* 110, 1842–1857. doi: 10.1016/S1388-2457(99)00141-8
- Qiu, N., Ma, W., Fan, X., Zhang, Y., Li, Y., Yan, Y., et al. (2018). Rapid improvement in visual selective attention related to action video gaming experience. *Front. Hum. Neurosci.* 12:47. doi: 10.3389/fnhum.2018.00047
- R Core Team (2018). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Rao, R. P. N. (2005). Bayesian inference and attentional modulation in the visual cortex. *Neuroreport* 16, 1843–1848. doi: 10.1097/01.wnr.0000183900.92901.fc
- Sauseng, P., Klimesch, W., Freunberger, R., Pecherstorfer, T., Hanslmayr, S., and Doppelmayr, M. (2006). Relevance of EEG alpha and theta oscillations during task switching. *Exp. Brain Res.* 170, 295–301. doi: 10.1007/s00221-005-0211-y
- Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., et al. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Curr. Biol.* 19, 1846–1852. doi: 10.1016/j.cub.2009.08.062
- Schenk, S., Lech, R. K., and Suchan, B. (2017). Games people play: how video games improve probabilistic learning. *Behav. Brain Res.* 335, 208–214. doi: 10.1016/j.bbr.2017.08.027
- Schmider, E., Ziegler, M., Danay, E., Beyer, L., and Bühner, M. (2010). Is it really robust? re-investigating the robustness of ANOVA against violations of the normal distribution assumption. *Methodology* 6, 147–151. doi: 10.1027/1614-2241/a000016
- Schubert, T., Finke, K., Redel, P., Kluckow, S., Müller, H., and Strobach, T. (2015). Video game experience and its influence on visual attention parameters: an investigation using the framework of the theory of visual attention (TVA). *Acta Psychol.* 157, 200–214. doi: 10.1016/j.actpsy.2015.03.005
- Schubert, T., and Strobach, T. (2012). Video game experience and optimized executive control skills—On false positives and false negatives: reply to Boot and Simons (2012). *Acta Psychol.* 141, 278–280. doi: 10.1016/j.actpsy.2012.06.010
- Shapiro, S. S., and Wilk, M. B. (1965). An analysis of variance test for normality (Complete Samples). *Biometrika* 52, 591–611. doi: 10.2307/2333709
- Spaak, E., Fonken, Y., Jensen, O., and de Lange, F. P. (2016). The neural mechanisms of prediction in visual search. *Cereb. Cortex* 26, 4327–4336. doi: 10.1093/cercor/bhv210
- Standley, D. (2018). *apaTables: Create American Psychological Association (APA) Style Tables. R package version 2.0.5*. Available at: <https://CRAN.R-project.org/package=apaTables> (accessed August 29, 2018).
- Strobach, T., Frensch, P. A., and Schubert, T. (2012). Video game practice optimizes executive control skills in dual-task and task switching situations. *Acta Psychol.* 140, 13–24. doi: 10.1016/j.actpsy.2012.02.001
- Tanaka, S., Ikeda, H., Kasahara, K., Kato, R., Tsubomi, H., Sugawara, S. K., et al. (2013). Larger right posterior parietal volume in action video game experts: a behavioral and voxel- based morphometry (VBM) study. *PLoS One* 8:e66998. doi: 10.1371/journal.pone.0066998
- van Dijk, H., van der Werf, J., Mazaheri, A., Medendorp, W. P., and Jensen, O. (2010). Modulations in oscillatory activity with amplitude asymmetry can produce cognitively relevant event- related responses. *Proc. Natl. Acad. Sci. U.S.A.* 107, 900–905. doi: 10.1073/pnas.0908821107
- Vangkilde, S., Bundesen, C., and Coull, J. T. (2011). Prompt but inefficient: nicotine differentially modulates discrete components of attention. *Psychopharmacology* 218, 667–680. doi: 10.1007/s00213-011-2361-x
- Wickham, H. (2016). *Ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer-Verlag.
- Wickham, H., François, R., Henry, L., and Müller, K. (2019). *dplyr: A Grammar of Data Manipulation. R Package Version 1.0.0*. Available at: <https://CRAN.R-project.org/package=dplyr> (accessed August 18, 2020).
- Wiegand, I., Hennig-Fast, K., Kilian, B., Müller, H. J., Töllner, T., Möller, H.-J., et al. (2016). EEG correlates of visual short-term memory as neuro-cognitive endophenotypes of ADHD. *Neuropsychologia* 85, 91–99. doi: 10.1016/j.neuropsychologia.2016.03.011
- Wiegand, I., Töllner, T., Dyrholm, M., Müller, H. J., Bundesen, C., and Finke, K. (2014a). Neural correlates of age-related decline and compensation in visual attention capacity. *Neurobiol. Aging* 35, 2161–2173. doi: 10.1016/j.neurobiolaging.2014.02.023
- Wiegand, I., Töllner, T., Habekost, T., Dyrholm, M., Müller, H. J., and Finke, K. (2014b). Distinct neural markers of TVA-based visual processing speed and short-term storage capacity parameters. *Cereb. Cortex* 24, 1967–1978. doi: 10.1093/cercor/bht071
- Wilke, C. O. (2019). *cowplot: Streamlined plot Theme and Plot Annotations for ggplot2. R Package Version 1.0.0*. Available at: <https://CRAN.R-project.org/package=cowplot> (accessed September 08, 2020).
- Wilms, I. L., Petersen, A., and Vangkilde, S. (2013). Intensive video gaming improves encoding speed to visual short-term memory in young male adults. *Acta Psychol.* 142, 108–118. doi: 10.1016/j.actpsy.2012.11.003
- Worden, M. S., Foxe, J. J., Wang, N., and Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific α -Bank electroencephalography increases over occipital cortex. *J. Neurosci.* 20, RC63–RC63. doi: 10.1523/JNEUROSCI.20-06-j0002.2000
- Wu, S., Cheng, C. K., Feng, J., D'Angelo, L., Alain, C., and Spence, I. (2012). Playing a first-person shooter video game induces neuroplastic change. *J. Cogn. Neurosci.* 24, 1286–1293. doi: 10.1162/jocn_a_00192
- Wu, S., and Spence, I. (2013). Playing shooter and driving videogames improves top-down guidance in visual search. *Attent. Percept. Psychophys.* 75, 673–686. doi: 10.3758/s13414-013-0440-2

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Copyright © 2020 Hilla, von Mankowski, Föcker and Sauseng. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

Alpha-tACS Alters Attentional Control but not Cognitive Functions as Video Games Do

- **Hilla**, Y., Link, F., & Sauseng, P (2022). Alpha-tACS alters attentional control but not cognitive functions as video games do: A psychophysical investigation based on the theory of visual attention. *European Journal of Neuroscience*, 57(10), 1705–1722.
- **Y.H.:** Conceptualization, Methodology, Project Administration, Investigation, Data Curation, Formal Analysis, Visualization, Software, Writing - Original Draft Preparation, Writing - Review & Editing. **F.L.:** Investigation, Data Curation. **P.S.:** Conceptualization, Funding Acquisition, Methodology, Resources, Supervision, Validation, Writing - Review & Editing.
- I developed the experimental design of this study. This included a comprehensive literature research and developing software to run the task. Moreover, I personally conducted the research. Furthermore, I analyzed the data and performed statistical tests. Furthermore, I wrote the manuscript to summarize the results of our research, and reviewed and edited the manuscript. Also, I took care of data curation, e.g., anonymization, etc.

Received: 27 July 2022 | Revised: 4 February 2023 | Accepted: 9 March 2023

DOI: 10.1111/ejn.15968

RESEARCH REPORT

EJN European Journal of Neuroscience FENSI WILEY

Alpha-tACS alters attentional control but not cognitive functions as video games do: A psychophysical investigation based on the theory of visual attention

Yannik Hilla^{1,2,3}  | Fabian Link¹ | Paul Sauseng¹

¹Department of Psychology, Ludwig-Maximilians-Universität (LMU), Munich, Germany

²Allgemeine Psychologie, Universität der Bundeswehr München, Neubiberg, Germany

³Graduate School of Systemic Neurosciences, Department of Biology II Neurobiology, Ludwig-Maximilians-Universität (LMU), Planegg, Germany

Correspondence

Yannik Hilla, Allgemeine Psychologie, Universität der Bundeswehr München, Werner-Heisenberg-Weg 39, 85577, Neubiberg, Germany.
Email: yannik.hilla@unibw.de

Funding information

This work was supported by Deutsche Forschungsgemeinschaft (grant number SA 1872/2-2).

Edited by: Gregor Thut

Abstract

Video game players' faster speed of information processing has been shown to coincide with altered posterior alpha power modulation, that is, brain oscillatory activity around 10 Hz. Thus, it was proposed that improved cognitive processing in video game players may be related to differential alpha activity. However, a causal relationship thereof has not yet been established. We addressed this by conducting a non-invasive brain stimulation study to demonstrate that modulating alpha power using transcranial alternating current stimulation (tACS) may impact on speed of information processing. Furthermore, we aimed to show that this effect correlated with altered attentional control, for example, visuospatial attention and/or top-down control processing, given that this has been suggested to contribute to video gaming effects. Therefore, we recruited 19 non-video game players to undergo one of five brain stimulation conditions while performing a visual short-term memory task at five different days, respectively. Thus, we applied tACS either at 10 Hz (alpha frequency) or at 16.18 Hz (control frequency) either over their left or right posterior parietal cortex (PPC) or a sham stimulation. Individuals' speed of information processing, visuospatial attention and top-down control processing were operationalised using a computational modelling approach based on the theory of visual attention. We found that alpha-tACS applied over individuals' left PPC altered their visuospatial attention orientation but not their speed of information processing. Thus, we were not able to establish a causal relationship between speed of information processing and altered visuospatial

Abbreviations: AICc, Second-Order Akaike Information Criterion; AOH, Activation-Orientation Hypothesis; BF₁₀, Bayes Factor (in Support of H1); BH, Benjamini-Hochberg (Method); BIC, Bayesian Information Criterion; DBSCAN, Density-Based Spatial Clustering of Applications with Noise; IAF, Individual Alpha Frequency; PPC, Posterior Parietal Cortex; rTMS, repetitive Transcranial Magnetic Stimulation; tACS, transcranial Alternating Current Stimulation; TVA, Theory of Visual Attention.

The work was conducted in a laboratory of the Department of Psychology at LMU.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2023 The Authors. *European Journal of Neuroscience* published by Federation of European Neuroscience Societies and John Wiley & Sons Ltd.

attention processing through alpha power modulation using non-invasive brain stimulation.

KEYWORDS

attentional control, brain stimulation, computational modeling, transfer effects

1 | INTRODUCTION

Video game players, that is, individuals who regularly play video games for several hours a week, appear to develop superior cognitive processing skills through playing video games. For instance, they have been shown to outperform non-video game players, that is, individuals not sharing this habit, in psychometric tasks operationalising attentional processing (Bediou et al., 2018; Green & Bavelier, 2003), perception (Li et al., 2010; Pohl et al., 2014), executive control (Cain et al., 2012; Green et al., 2012), memory (Blacker & Curby, 2013; McDermott et al., 2014) and probabilistic inference (Green et al., 2010; Schenk et al., 2017). Moreover, non-video game players displayed similar cognitive improvements after having participated in a video game training (Bejjanki et al., 2014; Blacker et al., 2014; Green et al., 2010; Green & Bavelier, 2003; Strobach et al., 2012). Thus, video gaming seems to impact not only on individuals' gaming performance but also inadvertently on their cognitive functions—a phenomena known as *transfer effect* (Perkins & Salomon, 1992).

The underlying mechanism thereof is not yet fully understood. Bavelier, Green, et al. (2012), for instance, suggested that video games might train individuals in developing efficient cognitive strategies by improving their *probabilistic inference*, that is, the ability to learn statistical regularities. Attentional control, the conjunction between attention and executive control functions to enable individuals to focus on processing relevant information while being able to suppress irrelevant information, may play a considerable role in this regard (Bavelier & Green, 2019). Bejjanki et al. (2014), for instance, showed that video game players did not outperform non-video game players in a psychometric task from the start on but after time on task; and that this effect, in turn, correlated with an increasing signal-to-noise ratio during information processing.

Furthermore, in support of this, video game players' superior cognitive processing correlated with alterations in neural substrates of attentional control functions (Bavelier, Achtman, et al., 2012; Föcker et al., 2018, 2019; Krishnan et al., 2013; Mishra et al., 2011; Tanaka et al., 2013; Wu et al., 2012). Hilla et al. (2020), for instance, found that video game players' faster speed of

information processing was associated with an increase in posterior parietal alpha amplitude attenuation in the course of time on task. Alpha activity refers to brain oscillatory activity around 10 Hz. It is widely considered as a neural substrate of attention processing given that its amplitude modulation coincides with differential information processing. Hereby, attenuated alpha activity appears to be associated with better and increased alpha activity with worse information processing, respectively (Capotosto et al., 2009; Jensen & Mazaheri, 2010; Peylo et al., 2021; Thut et al., 2006). Thus, Hilla and colleagues' (Hilla et al., 2020) results indicate that video game players' faster information processing might be related to them having been able to learn to deploy attention more efficiently than control individuals (see, Bavelier & Green, 2019).

However, this was just a correlational finding. Thus, it is not clear yet whether alpha power modulation may indeed impact on individuals' speed of information processing.

Furthermore, this alpha power modulation did not provide information which and how attentional control functions contributed to enhanced information processing (Hilla et al., 2020). To address these issues, we conducted a non-invasive brain stimulation study where non-video game players performed a visual short-term memory task at five different days and experienced one of five different stimulation conditions at each day. The aim of this study was to demonstrate that modulating posterior alpha activity using *transcranial alternating current stimulation* (tACS) may affect individuals' speed of information processing by impacting on their attentional control functions. Thus, we would imitate the video gaming effect previously described (Hilla et al., 2020) and acquire indirect evidence indicating that the conjunction between alpha power modulation and altered attentional control may account for enhanced cognitive processing as observed in video game players (Bavelier & Green, 2019). We used tACS therefore because it represents an established non-invasive brain stimulation method to alter brain oscillatory activity (Herrmann et al., 2016). Moreover, applied at alpha frequency over the posterior parietal cortex (PPC), it has been shown to reliably modulate visuospatial attention processing—an essential cognitive control function (Helfrich et al., 2014;

Kemmerer et al., 2022; Vogeti et al., 2022). Furthermore, similar to Hilla and colleagues (Hilla et al., 2020), we operationalised individuals' speed of information processing by means of a computational modelling approach based on the *theory of visual attention* (TVA) (Bundesen et al., 2015; Dyrholm et al., 2011; Kyllingsbæk, 2006). Likewise, their attentional control functions were operationalised by means of TVA visuospatial attention and top-down control parameter values.

Besides that, we modelled and investigated individuals' TVA visual short-term memory capacity. This was because TVA visual short-term memory capacity was likely affected by tACS as well given that, firstly, short-term memory performance has been shown to be related to alpha activity (Riddle et al., 2020; Sauseng et al., 2009). Secondly, TVA speed of information processing and short-term memory capacity are highly correlated (Finke et al., 2005). Thus, differential TVA visual short-term memory capacity likely coincides with altered speed of information processing through alpha power modulation. In this regard, in particular right hemispheric brain stimulation might induce alterations in TVA cognitive processing. In support of this, Hung et al. (2005), Kraft et al. (2015) and Moos et al. (2012) showed that TVA visual short-term memory capacity and top-down control were modulated by right but not left hemispheric posterior brain stimulation.

Thus, we hypothesised that tACS applied at alpha frequency (10 Hz) over individuals' PPC would alter their TVA speed of information processing (**H1**) (Hilla et al., 2020). Moreover, we expected this effect to be related to alterations in TVA visuospatial attention and/or top-down control processing (**H2**) (Bavelier & Green, 2019; Kemmerer et al., 2022). In addition to that, we anticipated that differential TVA short-term memory capacity may coincide with these effects (**H3**) (Finke et al., 2005; Riddle et al., 2020; Sauseng et al., 2009). Furthermore, we expected that these effects might be more pronounced as result of right than left hemispheric tACS application (**H4**) (Hung et al., 2005; Kraft et al., 2015; Moos et al., 2012).

2 | METHODS

2.1 | Participants

We estimated that 18 individuals were required to achieve a statistically significant effect, assuming a moderate effect size ($eta_p^2 = .10$) with a statistical power of 80% and a chance of committing a Type I error of 5% in a repeated measures design where each individual's performance would be measured five times (Campbell &

Thompson, 2012). Thus, we recruited 19 healthy volunteers to participate in experiments at five different days; that is, 95 test sessions were run in total ($N_{female} = 9$; $N_{male} = 10$). At each day, they performed a visual short-term memory task and experienced one of five different brain stimulation conditions. Participants were between 19 and 30 years old ($M = 23$; $SD = 2.54$). All except for one individual with mixed handedness were right handed (Veale, 2014). Moreover, most of them were undergraduate students ($N_{Undergraduate} = 10$; $N_{Bachelor's Degree} = 6$; $N_{Training} = 1$; $N_{Master's Degree} = 1$; $N_{PhD} = 1$) and pursued studies foremost in Social Sciences, for example, Psychology ($N_{Social Sciences} = 11$; $N_{Medicine} = 4$; $N_{Humanities} = 1$; $N_{Natural Sciences} = 1$; $N_{Technology} = 1$; $N_{Not a student} = 1$). The local ethics review board approved this study. All volunteers provided written informed consent in line with the Declaration of Helsinki, and all volunteers were compensated for their participation either with money or student lab tokens.

2.2 | Materials and procedures

2.2.1 | Inclusion criteria and demographic data acquisition

Only healthy individuals between 18 and 40 years of age with normal or corrected-to-normal vision who fulfilled the criteria of non-video game players were eligible to participate in this study (Green et al., 2017; Large et al., 2019). All individuals were thoroughly screened for (1) any history of seizures, epilepsy, fainting or traumatic brain injury, (2) any type of metal objects in their body (though retainers and dental fillings were allowed) and (3) residual risk factors, such as a history of surgery on their spine, drug/alcohol or medication intake, tinnitus, pregnancy or sleep deprivation. Only if none of these factors applied to an individual were they allowed to participate in the experiments.

2.2.2 | Task

We developed a visual short-term memory task by means of *Python's Tkinter* library¹ and run it using the *Spyder* IDE² on a computer with an AMD AthlonTM II X2 B24 processor (AMD, Sunnyvale, CA, United States) and a 64-Bit Windows 7 operating system (Microsoft, Redmond, WA, United States). Stimuli were presented on a 17"/43 cm monitor (Acer Group, Taiwan) with a refresh

¹<https://wiki.python.org/moin/TkInter>

²<https://www.spyder-ide.org/>

rate of 60 Hz, whereas participants sat approximately 80 cm distant from this screen on a comfortable chair in a darkened room.

The participants performed the same visual short-term memory task at each day while one of five different brain stimulation protocols was applied simultaneously. The visual short-term memory task comprised a training and two blocks of experimental trials where individuals had to memorise two white shapes that were depicted on a virtual circle (radius of 2.72° of visual angle) either in the left or right visual field, either with or without black shapes as distractors at one of three different exposure durations. In detail, each trial started with the presentation of a blank screen. After 1002 ms, a white fixation cross ($.72^\circ \times .72^\circ$ of visual angle) appeared in the centre of the screen. We asked the participants to focus their attention to this fixation cross. After additional 1002 ms, a memory display was depicted. A memory display always contained two unique white shapes and in half of the trials two unique white shapes and four unique black shapes (approximately $2.08^\circ \times 2.08^\circ$ of visual angle). We asked the participants only to memorise white and to ignore black shapes. These shapes could be an ellipse, a diamond, a pentagon, a rhombus, a square, a trapezoid or a triangle. Shapes were depicted at 210° , 270° and 330° in the left or at 30° , 90° and 150° in the right visual field, respectively. But white shapes were presented either only in the right or left visual field. After 66.8, 100.2 or 133.6 ms, a memory display was substituted by a mask display. This comprised white squares at each location where a shape could have been presented with random black polygons depicted on them ($2.29^\circ \times 2.29^\circ$ of visual angle). After another 501 ms, the participants were instructed to report which shapes they memorised by pressing keys marked with the corresponding shapes. Therefore, we marked keys with luminescent stickers. Thus, an ellipse was glued on key “f”, a diamond on key “g”, a pentagon on key “h”, a rhombus on key “j”, a square on key “v”, a trapezoid on key “b” and a triangle on key “n”, respectively. These stickers served as a reference guide.

Thus, the participants were not required to learn button-to-stimulus response mappings. The participants were not supposed to guess. They were allowed to refrain and could indicate between one and two shapes. There was no response time limit. The participants started the next trial by pressing the space key. For a visualisation of the task, see Figure 1. One training comprised 24 trials. Training trials differed from experimental ones by providing feedback after each response: if the participants refrained or indicated at least one incorrect shape during a training, a black “X” ($.93^\circ \times .93^\circ$ of visual angle) was presented in the centre of the screen for 501 ms after the

space key had been pressed. But this was not the case during the experiment. Individuals were allowed to conduct up to two trainings at the first day and one training on each following testing session. Then, the participants performed two blocks of 252 experimental trials, that is, 504 experimental trials in total. There were 21 unique combinations how shape stimuli could have been paired in a memory display (e.g. ellipse and square). These pairs could then either be presented in the left or right visual field and either on their own or with four additional black distracting shapes. To ensure that each shape was equally often presented at each position in the visual field, target pairs were displayed according to three conditions in each visual field both in normal and reversed order, for example, ellipse at the upper and square at the lower position of the left visual field, and vice versa. Thus, there were 504 possible memory display combinations (42 shape pairings [normal and reversed order] distributed across six location conditions [three in both visual fields] and presented either on their own or with distractors). Presenting each memory display at each exposure duration would have resulted in 1512 experimental trials. On average, individuals would have worked for 3 h on this task. Moreover, individuals would have undergone approximately 3 h of brain stimulation—which we considered unreasonable. Therefore, memory displays were randomly but evenly associated with exposure durations. Thus, all participants performed 252 trials where memory displays had been presented with targets in either the left or right visual field and with or without distractors at each testing session, respectively. Moreover, all participants performed 168 trials where memory displays had been presented at 66.8, 100.2 or 133.6 ms. Note that the trial number of each condition (e.g. memory displays with targets presented in the left visual field without distractors at the longest exposure duration) differed slightly within and between individuals and between testing sessions given that exposure durations were randomly assigned to memory displays. Crucially, these differences were not significant.³ Thus, potential performance differences across conditions were unlikely related to different numbers of trials of experimental conditions. Furthermore, the order of memory displays was always random. Thus, the participants were not able to anticipate either the identity or location of target shapes or the condition or exposure duration of a memory display.

The participants had sufficient opportunities to make breaks. This was because, firstly, there was no response time limit but a new trial was started by pressing the space key. Secondly, we asked the participants to make a

³Please review the **Task** section of our supporting information for more details on conditional trial distributions.

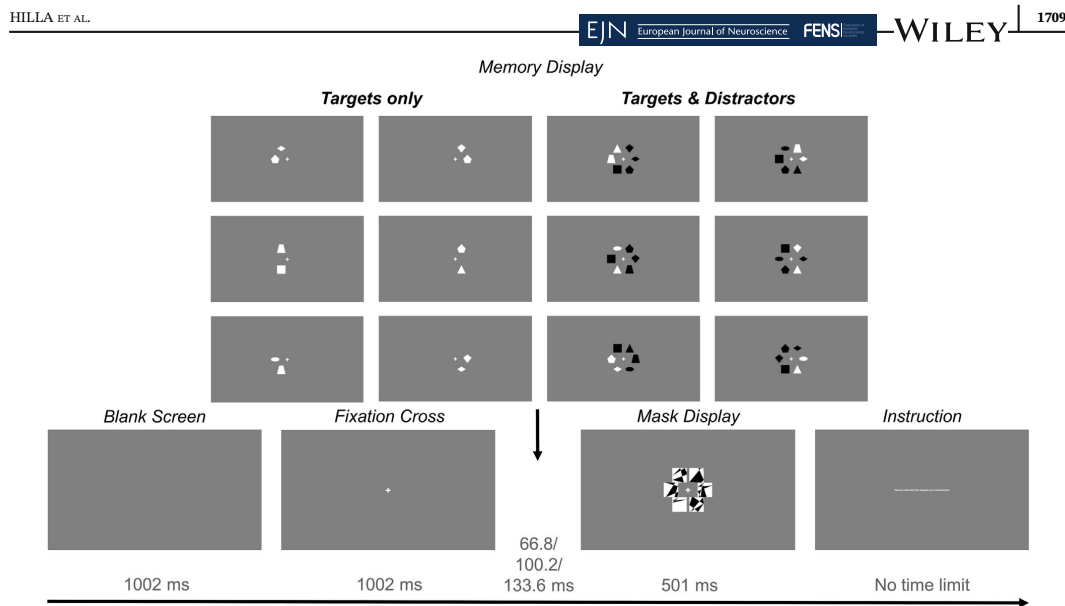


FIGURE 1 Participants performed a visual short-term memory task where they memorised white shapes depicted on an invisible circle either in the left or right visual field, either with or without black shapes as distractors at one of three different exposure durations. There were always two white shapes regardless of memory display condition. Memory displays were subsequently masked by white squares with random black polygons depicted on them to prevent afterimages. At the end of each trial, the participants were asked to indicate which shapes they memorised by pressing keys on a regular keyboard marked with corresponding shapes. There was no response time limit. Each new trial was initiated by pressing the space key. At the onset of each trial, a blank gray screen was shown. After 1002 ms, a white “+” was depicted in the centre of the screen to which the participants were supposed to focus their gaze to. After 1002 ms, a new memory display was shown.

longer break between experimental blocks. No brain stimulation was applied during these longer breaks.

2.3 | Theory of visual attention cognitive functions

2.3.1 | Parameter value estimation

We operationalised visual short-term memory capacity (K), visual speed of information processing (C), a temporal threshold for conscious information processing (effective exposure duration; t_0), top-down control (α) and visuospatial attentional processing (*spatial bias*) by means of a computational modelling approach based on TVA (Bundesen et al., 2015; Dyrholm et al., 2011; Kyllingsbæk, 2006). Parameter values reflecting these cognitive functions were estimated based on performance in different task conditions using maximum likelihood method.

K parameter values (visual short-term memory capacity) were computed from accuracy data in response to memory displays presented at different exposure

durations and based on different set sizes using a mass function as described in Equation (1) (Dyrholm et al., 2011; Kyllingsbæk, 2006). Hereby, i indicates an individual, j the number of items that may be memorised, n the total number of items presented in the visual field and P the probability for memorising j items.

$$K_i = \sum_{j=1}^n P(j) \times j \quad (1)$$

C and t_0 parameter values (speed of information processing; effective exposure duration) were computed from accuracy data in response to memory displays presented at different exposure durations as well (Dyrholm et al., 2011; Kyllingsbæk, 2006). The idea underlying the modelling approach of these three parameters is that the number of memorised items should increase exponentially as a function of exposure duration: the longer the exposure duration, the easier the encoding, the more likely targets may be memorised.

Thus, the probabilities P for memorising j items depend on how many items j had been correctly recalled

at each exposure duration (but see, Dyrholm et al. [2011], for more information on this relationship). Consequentially, the asymptotic level of this function indicates the visual short-term memory capacity, K ; its starting point the minimum exposure duration required for conscious information processing, t_0 ; and the gradient parameter of its slope line visual speed of information processing, C . Temporal precision is crucial here. Thus, we applied masks to prevent visual afterimages. On top of that, we controlled for temporal imprecision related to operations run on non-real time operating systems by computing the mode value of distributions of difference values between predicted and observed time delays between stimuli applying the `default_timer` function of Python's `timeit` library.⁴ Thus, we corrected for temporal imprecision by adding respective mode difference values to the predicted exposure durations. Consequentially, 66.8, 100.2 and 133.6 ms were changed to 71.2, 106.8, and 126.8 ms for computational modelling (see Hilla et al. (2020) for a similar approach).

TVA α parameter values (top-down control) were computed from differences in accuracy data in response to trials where either only targets or targets and distractors had been displayed in memory displays, see Equation (2) (Dyrholm et al., 2011; Kyllingsbæk, 2006). An individual i with high top-down control should allocate attention resources w stronger to targets than distractors resulting in a larger ratio between the two conditions as compared to an individual i with lower top-down control. Thus, α values range between 0 and 1 with 0 indicating high top-down control and 1 similar attentional weighting in both conditions. We then applied a log10-transformation on α values after adding 1 as a constant to enable linear comparisons. As a result, α values ranged between 0 and .30 with 0 suggesting high and .30 low top-down control.

$$\alpha_i = \frac{w_{\text{distractors}_i}}{w_{\text{targets}_i}} \quad (2)$$

TVA *spatial bias* values were computed from differences in accuracy data in response to targets presented at different spatial locations in memory displays (Dyrholm et al., 2011; Kyllingsbæk, 2006). Hereby, attentional weights w were estimated for every position depending on how well the participants responded to these spatial locations. We then put the attentional weights of stimuli presented in the left visual field in relation to those displayed in the right to compute a *spatial bias*, see Equation (3). Hereby, i indicates an individual and w an attentional weight of either the left (j) or right (k) visual

field. Values $> .5$ indicate a leftward and values $< .5$ a rightward *spatial bias*.

$$\text{Spatial Bias}_i = \frac{\sum_{j=1}^3 w_{ji}}{\sum_{j=1}^3 w_{ji} + \sum_{k=1}^3 w_{ki}} \quad (3)$$

2.3.2 | Differential model assumptions: balanced vs. biased visuospatial attentional processing

TVA parameter values may be estimated under the assumptions that attentional resources are either distributed homogeneously, that is, *balanced*, or *biased* in the visual field. In theory, healthy individuals' performances should fit well to a *balanced* model given that they should be able to allocate attentional resources homogeneously in the visual field. Nevertheless, it has also been frequently reported that healthy individuals display a visuospatial bias (Brooks et al., 2014). Thus, their performance may be fit to both model assumptions.

However, such model fit assumptions may impact on TVA parameter estimation beyond attentional resource allocation resulting in divergent parameter estimates. K parameter estimation, for instance, depends on set sizes of memory displays (Dyrholm et al., 2011; Kyllingsbæk, 2006). Given a *balanced* model, probabilities P for memorising j items may be computed based on the assumption that individuals memorise up to two targets irrespective of their spatial location in the visual field. In contrast, provided a *biased* model, these probabilities P may be computed based on the assumptions that targets had been presented at six different locations and either with or without distractors. Consequentially, probabilities P might be largest for memorising 0, 1 or 2 items given a *balanced* model, whereas they may be largest for memorising more than two items provided a *biased* model. Thus, K parameter values may be overestimated given a *biased* as compared to a *balanced* model. Furthermore, for similar reasons TVA α parameter value estimates might differ depending on model assumptions. These are computed based on performance in response to memory displays with targets only as compared to targets and distractors. Given a *balanced* model, combinations of these conditions (e.g., targets presented at six different spatial locations) may be neglected. In contrast, provided a *biased* model, attentional weighting towards targets presented at different spatial locations and either with or without distractors is accounted for. Thus, α estimates might diverge. Therefore, we conducted a series of control analyses to determine which

⁴<https://docs.python.org/3.7/library/timeit.html>

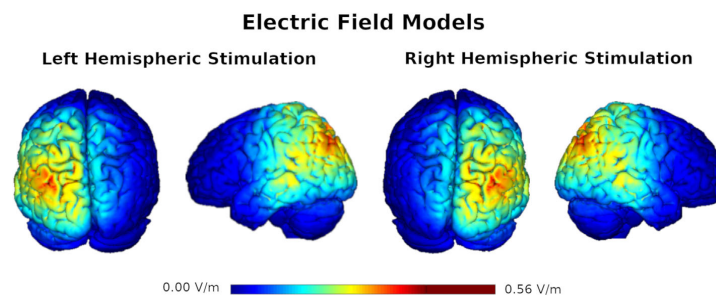


FIGURE 2 Electric field model(s). (left side) Simulation of an electric field generated in the left hemisphere by mounting a stimulation electrode at P3 and return electrodes at Oz, Cz and T7, respectively. (right side) Simulation of an electric field generated in the right hemisphere by mounting a stimulation electrode at P4 and return electrodes at Oz, Cz and T8, respectively. The magnitude of the electric field is indicated in $|E|$.

estimates (based on a *balanced* or *biased* model) should be used for further analyses.⁵

As a result, we chose to use TVA estimates based on the *biased* TVA model because individuals' performances fit best to this model (as determined based on *AICc* values). However, there were three exceptions: (1) *K* parameter estimates were based on the *balanced* model because they appeared to have been overestimated based on the *biased* model; (2) data of three testing sessions fit better to the *balanced* than the *biased* model; and (3) there were five cases where the deviation between estimates given a *biased* and a *balanced* model were unreasonably large because of extreme values of the *biased* model (two cases for *t0* and three cases for *C* estimates). Therefore, we substituted these estimates by estimates of the *balanced* model.

2.3.3 | Brain stimulation

We used a NE[®] starstim tACS device (Neuroelectronics[®], Barcelona, Spain) and four electrodes mounted in a neoprene cap to apply tACS *online* at 2000 μ A (zero-to-peak intensity). There were five different stimulation conditions: *Condition 1*: 10-Hz stimulation applied to the left PPC; *Condition 2*: 10-Hz stimulation applied to the right PPC; *Condition 3*: 16.18-Hz stimulation applied to the left PPC; *Condition 4*: 16.18-Hz stimulation applied to the right PPC; and *Condition 5*: sham stimulation applied over the medial superior parietal cortex. *Online* means that the stimulation was applied throughout the whole time while participants performed the task. The stimulation started directly before the participants started performing experimental trials and was stopped after they

had performed the last experimental trial. Each stimulation was applied on a different day. Hereby, we determined all possible unique combinations of conditions per day and randomly selected one such stimulation protocol for each participant. Thus, each participant experienced a unique stimulation protocol. There was no indication that either one of the stimulation conditions was applied more frequently on a specific day as compared to other days. Thus, it is rather unlikely that order effects confounded our data. For left hemispheric stimulation, the stimulation electrode was mounted at electrode site P3, and return electrodes were mounted at electrode sites Oz, Cz and T7. In contrast for right hemispheric stimulation, the stimulation electrode was mounted at electrode site P4 and return electrodes were mounted at electrode sites Oz, Cz and T8.⁶ As can be inferred from Figure 2, these protocols should have resulted in a fairly focal stimulation of the parietal cortex (Bender et al., 2019; Helfrich et al., 2014; Moliadze et al., 2019; Wolinski et al., 2018). For sham stimulation, the stimulation electrode was positioned at electrode site Cz and return electrodes were mounted at electrode sites P3, Oz and T7. Hereby, a stimulation of 16.18 Hz was ramped up at the onset of experimental trials but ramped down again after 3 s and did not further continue throughout the experiment. After their final session, the participants were informed of the aim of this study and asked to indicate at which day sham stimulation may have been applied. None of the individuals were able to correctly indicate this. Moreover, none of the individuals reported differential sensations during testing sessions. Thus, we are confident that their

⁵See **Methods** in supporting information for more details.

⁶For the interested reader, see **Brain Stimulation** in supporting information, for a discussion why alpha-tACS applied at 10 Hz as compared to an individual alpha frequency (IAF) was sufficient for our research purpose.

performance had been unlikely affected by expectation effects.

2.4 | Statistical analyses

2.4.1 | Model fitting

We computed hierarchical generalised (linear/additive) regression models to test our hypotheses. Hereby, *stimulation condition* (Condition 1 vs. Condition 2 vs. Condition 3 vs. Condition 4 vs. Condition 5), *target position* (left vs. right), *trial type condition* (targets only vs. targets and distractors), *exposure duration* (71.2 ms vs. 106.8 ms vs. 128.6 ms), TVA *K* (short-term memory capacity), *C* (speed of information processing), *t0* (effective exposure duration), α (top-down control), and *spatial bias* (visuospatial attention) parameter values and individuals' *error rate* represented variables of interest.

However, we only analysed *t0* for exploratory reasons given that we had no strong hypothesis how tACS might impact on this parameter. We determined the significance of a model by comparing its second-order Akaike information criterion (*AICc*) value to the *AICc* value of a reference model. Smaller *AICc* values indicate a better model fit than larger ones. Thus, $\Delta AICc$ values > 2 suggest a significant model fit difference (Burnham & Anderson, 2004). For instance, in order to test whether there were differential effects of tACS conditions on TVA speed of information processing, one would compare the *AICc* value of a model comprising *stimulation condition* as predictor variable and TVA *C* parameter values as criterion variable with the *AICc* value of a model without predictor variable. The latter is also referred to as *intercept* model given that its model fit depends on its mean/intercept value only. If the *AICc* value of the former model was at least two units smaller than the *AICc* value of the latter model, this would indicate that *stimulation condition* explained a significant portion of the variance of TVA *C* parameter values. In contrast, in order to test whether an interaction between two predictors, for example, *target position* and *exposure duration*, explained a significant portion of a criterion variable, for example, *error rate*, one would need to compare a model comprising both the main effects *target position* and *exposure duration* and the interaction term between *target position* and *exposure duration* to a model comprising only the main effect terms *target position* and *exposure duration*. Thus, it would be possible to disentangle the interaction effect from the main effects. Furthermore, it is possible to introduce random effects to these models. Random effects represent variables that may possibly explain some variance of the criterion variable but are not of primary research

interest. For instance, there may be intra-individual differences between testing sessions given that individuals' activity levels may fluctuate or because some are faster learners than others. Introducing these variables, for example, *subject* and *day*, to a model allows to control for their contribution to the dependent variable, meaning that the influence of predictors of interest may be estimated more precisely. This is because, the influence of *stimulation condition* would not only be estimated based on different levels of *stimulation condition* but also depending on individuals' performance in general and the performance displayed at different days. In addition to that, random effects may also be considered for slope estimations in models with metric predictors, for example, with TVA *C* parameter values as predictor and TVA *K* parameter values as criterion variables. Thus, the relationship between TVA parameter values would be estimated by allowing for differential relationships for each individual and/or at each day. Importantly, for comparing models with random effects, both the reference model and model of interest need to contain the random effects. Besides that, model fits between different models may be compared to each other to determine which model explains a criterion best.

2.4.2 | Bayesian statistics

In addition to that, we computed *Bayes factors* (BF_{10}) based on *Bayes information criterion* (*BIC*) values in order to determine how strong the data favoured a model of interest over a reference model using Equation (4) by Wagenmakers (2007). For instance, $BF_{10} = 3$ indicates that data fit three times more likely to a model of interest as compared to the corresponding reference model. However, model fits as operationalised by means of $\Delta AICc$ and BF_{10} values do not necessarily match since *BIC* values are differently penalised than *AICc* values (Stoica & Selen, 2004). Thus, we considered a model fit as significant only if $\Delta AICc > 2$ and $BF_{10} > 1$.

$$BF_{10} = \exp((BIC_{\text{reference}} - BIC_{\text{model of interest}})/2) \quad (4)$$

2.4.3 | Post-hoc processing

The range of most plausible estimates of linear regression coefficients was then determined by computing two-tailed confidence intervals whose significance level, $\alpha = .05$, was adjusted by means of *Benjamini-Hochberg* (*BH*) procedure if necessary, see Equation (5)

(Benjamini & Hochberg, 1995).⁷ Moreover, the significance of condition-specific smooth terms was determined by means of F -test statistics where p -values were also corrected by applying the BH -procedure if necessary.

$$CI_{BH} = \left[\bar{y} \pm t_{\left(1 - \frac{\text{rank} \times \alpha}{n_{\text{tests}} \times 2}; n_{\text{observations}} - (df_{\text{parametric}} + df_{\text{smooth}}) - 1\right)} \times \text{se}(y) \right] \quad (5)$$

The range of most plausible average estimates reported, for example, for descriptive statistical reasons, were determined by computing two-tailed confidence intervals with a significance level of .1%, see Equation (6).

$$CI_{\text{descriptive}} = \left[\bar{y} \pm t_{\left(1 - \frac{\alpha}{2}; n_{\text{observations}} - 1\right)} \times \text{se}(y) \right] \quad (6)$$

2.4.4 | Model assumptions and constraints

We controlled for outliers in regression models with smooth terms by applying the *density-based spatial clustering of applications with noise (DBSCAN)* algorithm (Ester et al., 1996). Hereby, clusters contained at least five data points, and their radius was constrained to distance values $< Q_3 + 3 * IQR$. We only analysed models further if there were less than 5% outliers.

Moreover, we only reported models if their model fits were significant, $\Delta AICc > 2$ and $BF_{10} > 1$, based on both full data and data without outliers.

Furthermore, we controlled if residuals were fairly symmetrically distributed applying the following procedure: at first, we estimated location and scale parameter values given a normal distribution based on residual values using maximum likelihood method. Then, we determined the frequency of each residual value rounded to the second decimal. Afterwards, we computed the probability of these residual values by dividing these frequencies by the total amount of unique residual values. In a next step, we accumulated these probabilities in an ascending order corresponding to the order of the residual values to model the progression of a cumulative distribution function. Subsequently, we indeed modelled a normal cumulative distribution function based on the location and scale parameter estimates we had acquired using maximum likelihood method. Thus, we were able to determine the most plausible deviation between

observed and predicted cumulative probabilities of residual values given a normal distribution assumption using confidence intervals with a significance level of 5% (CI_{Gauss}). We did not determine the model fit based on whether 0 was among these most plausible values. Firstly, this approach would be counter-intuitive to frequentist testing. Secondly, 0 may be unlikely among the most plausible values the better the model fit given that the corresponding standard error may be small and hence the range of the confidence interval narrow. Alternatively, we will report the size of the range of the most plausible values ($\text{range size}_{\text{Gauss}}$). There is no rule of thumb which range size indicates a good model fit and thus implies symmetrically distributed residuals. Nevertheless, we believe that a range size of up to 5% may suggest a very good, between 5% and 10% a good, and between 10% and 15% an acceptable fit.

On top of that, we controlled whether residuals were homoscedastic using the following approach: we fitted generalised additive models with z -standardised residuals as criterion and z -standardised predicted values as predictor variables with random intercepts and slopes for each individual and each day (if applicable) and compared the model fit to a reference model with random intercepts and slopes for each individual and each day (if applicable). If $\Delta AICc > 2$ and $BF_{10} > 1$, we considered a model as problematic and did not report it.

2.4.5 | Individuals' performance

We then investigated which stimulation and conditional factors impacted on individuals' performance in the visual short-term memory task the most. For this, we conducted hierarchical regression analyses with *error rate* as criterion variable, and *stimulation condition* (Condition 1 vs. Condition 2 vs. Condition 3 vs. Condition 4 vs. Condition 5), *target position* (left vs. right), *trial type condition* (targets only vs. targets and distractors) and *exposure duration* (71.2 ms vs. 106.8 ms vs. 126.8 ms) as predictor variables with random intercepts for each individual and for each day.

2.4.6 | TVA parameter values

Furthermore, we analysed whether different brain stimulation protocols impacted on TVA cognitive functions relative to sham condition by conducting hierarchical regression analyses with K (short-term memory capacity), C (speed of information processing), $t0$ (effective exposure duration), α (top-down control) and *spatial bias* parameter values as criterion variables and *stimulation*

⁷Note that we did not consider intercepts for these computations as we were primarily interested in significant differences between conditions.

condition (Condition 1 vs. Condition 2 vs. Condition 3 vs. Condition 4 vs. Condition 5) as predictor variable with random intercepts for each individual and for each day.

2.4.7 | Associations between TVA parameter values

Moreover, we investigated whether associations between TVA parameter values were differently affected by stimulation condition as compared to sham condition. For this, we computed hierarchical generalised additive models with K , C , $t0$, α and *spatial bias* parameter values as criterion variable, either one of the remaining parameter values as predictor variable, and *stimulation condition* (Condition 1 vs. Condition 2 vs. Condition 3 vs. Condition 4 vs. Condition 5) as grouping variable with random intercepts and slopes for each individual. We also conducted these analyses with *day* (1 vs. 2 vs. 3 vs. 4 vs. 5) as grouping variable. If the latter model fits were significant, we did not include *day* as a random effect variable.

2.4.8 | Software

Data analyses were conducted using *R* (R Core Team, 2022; Version 4.2.2). Data were (pre-)processed using the *dplyr* and *tidyr* packages (Wickham, 2021; Wickham et al., 2021). Binomial tests were conducted using the *rstatix* package (Kassambara, 2021) (see supporting information for application examples).

Regression models were fit and processed by means of the *mgcv* and *tidymv* packages (Coretta, 2021; Wood, 2011). *AICc* values were computed using the *MuMIn* package (Barton, 2020). To employ outlier detection, we used the *dbscan* and *factoextra* packages (Hahsler et al., 2019; Kassambara & Mundt, 2020). To estimate location and scale parameters of a normal distribution using maximum likelihood method, we applied the *optim* algorithm of *R*'s *stats* package (R Core Team, 2022). For data visualisation, we used the *ggplot2*, *patchwork*, *RColorBrewer*, and *kableExtra* packages (Neuwirth, 2014; Pedersen, 2020; Wickham, 2016; Zhu, 2021).

3 | RESULTS

3.1 | Individuals' performance

Individuals' performance was best explained by a model comprising *target position*, *trial type condition* and *exposure duration* as interaction term with random intercepts for each individual and each day irrespective of the

stimulation protocol ($\Delta AICc = 69.54$, $BF_{10} > 100$, $CI_{Gauss} = [.00; .02]$, *range size*_{Gauss} = 1.63%).⁸ On average, they displayed the lowest mean error rate of between 1.67 and 7.97% in response to targets presented in the right visual field without distractors at the longest exposure duration. Their mean error rate was on average between .36 and 5.69% larger in response to memory displays with distractors. Moreover, their mean error rate was on average between 1.50 and 7.13% larger in response to memory displays presented at the shortest exposure duration. In addition to that, their mean error rate increased further by on average between 5.29 and 13.93% if targets had been presented in the left visual field at the shortest exposure duration. All remaining effect terms were unlikely to contribute to explaining individuals' performance as the respective confidence intervals contained 0, see Table 1. For a visualisation of these effects, see Figure 3.

3.2 | TVA parameter values

Only the model with *spatial bias* values as criterion variable and *stimulation condition* as categorical predictor variable with random intercepts for each individual and each day reached significance ($\Delta AICc = 4.19$, $BF_{10} = 2.22$, $CI_{Gauss} = [.01; .03]$, *range size*_{Gauss} = 1.99%). Individuals' spatial bias values ranged on average between .04 and .35 in the sham condition. Thus, the participants seemed to have deployed attentional resources stronger to the right visual field given that spatial bias values $< .5$ indicate a rightward and values $> .5$ a leftward bias. Interestingly, only tACS applied to the left PPC at alpha frequency (10 Hz) modulated this effect as individuals' spatial bias values were on average between .02 and .18 values larger in Condition 1 as compared to Condition 5. Thus, left hemispheric alpha-tACS applied to the left PPC appeared to have caused a reduction of a rightward spatial bias towards more balanced attentional processing in the majority of subjects. For a visualisation of this effect, see Figure 4.⁹

3.3 | Associations between TVA parameter values

Moreover, only the model comprising α values as criterion variable and *spatial bias* values as predictor

⁸ $\Delta AICc$ and BF_{10} values were computed in comparison to *AICc* and *BCI* values of two different second best models.

⁹For a visualization of the impact of all tACS protocols on *spatial bias* values, see **Results** in supporting information.

TABLE 1 Generalised linear model with error rate as criterion and target position (left vs. right), trial type condition (targets only vs. targets and distractors) and exposure duration (71.2 ms vs. 106.8 ms vs 126.8 ms) as predictors and subject and day as random effects.

Regression coefficients	Lower bound	Upper bound
Target position (left) × exposure duration (71.2 ms)	.05289	.13931
Exposure duration (71.2 ms)	.01504	.07130
Trial type condition (targets and distractors)	.00362	.05687
Target position (left) × trial type condition (targets and distractors) × exposure duration (71.2 ms)	−.00334	.09879
Trial type condition (targets and distractors) × exposure duration (71.2 ms)	−.00658	.06308
Target position (left) × trial type condition (targets and distractors)	−.01011	.05745
Target position (left) × exposure duration (106.8 ms)	−.01057	.05517
Trial type condition (targets and distractors) × exposure duration (106.8 ms)	−.00999	.05415
Target position (left) × trial type condition (targets and distractors) × exposure duration (106.8 ms)	−.02975	.05891
Exposure duration (106.8 ms)	−.01530	.02810
Target position (left)	−.01538	.02717

Note: Lower/upper bound: Benjamini–Hochberg-corrected confidence interval boundaries.

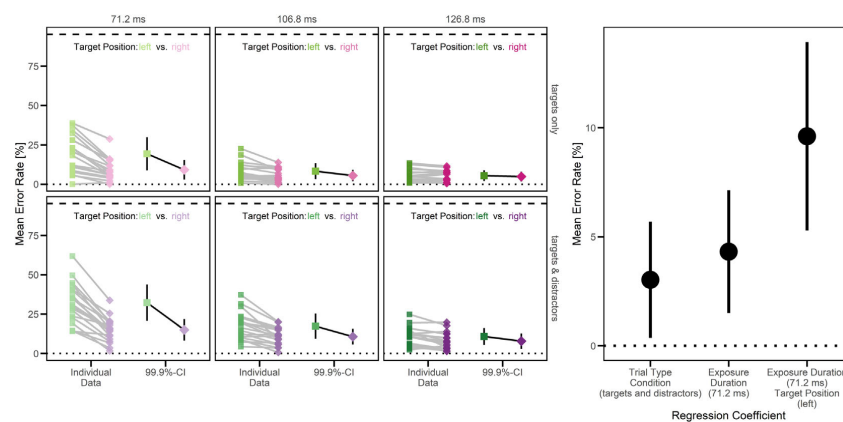


FIGURE 3 Individuals' performance. Performance was operationalised by (mean) error rate. Individuals' error rates in response to stimuli presented at different positions in the visual field (left vs. right), without and with distractors (targets only vs. targets and distractors) and at different exposure durations (71.2 ms vs. 106.8 ms vs. 126.8 ms) are illustrated by different colours, shapes, luminance and transparency values. Target position contrasts are indicated by green squares and pink diamonds; trial type condition contrasts by differences in luminance; and exposure duration contrasts by different levels of transparency. The black dashed line indicates P (at least one incorrect). (left panel) Individuals' mean error rate in each condition averaged over stimulation conditions and corresponding 99.9% confidence intervals. (right panel) Regression coefficients: individuals' error rate increased in response to memory displays with distractors and in response to memory displays presented at the shortest exposure duration—in particular if targets had been presented in the left visual field. Dots indicate averages, and whiskers Benjamini–Hochberg-corrected confidence intervals.

variable with random intercepts and slopes for each individual reached significance when fit for each stimulation condition, separately ($\Delta AICc = 10.76$, $BF_{10} > 100$, $CI_{Gauss} = [-.01; .12]$, $range\ size_{Gauss} = 12.27\%$). Hereby, all conditional fits were significant, $p_{SBH} < .001$. As can be inferred from Figure 5, there appeared to be a linear association between the two variables in

Condition 5 (sham condition). This indicates that on average individuals allocated attentional resources stronger to targets than distractors if presented in the right visual field than the left one at the baseline. Interestingly, there were very similar trajectories describing the association between the two variables for each brain stimulation condition. Thus, tACS

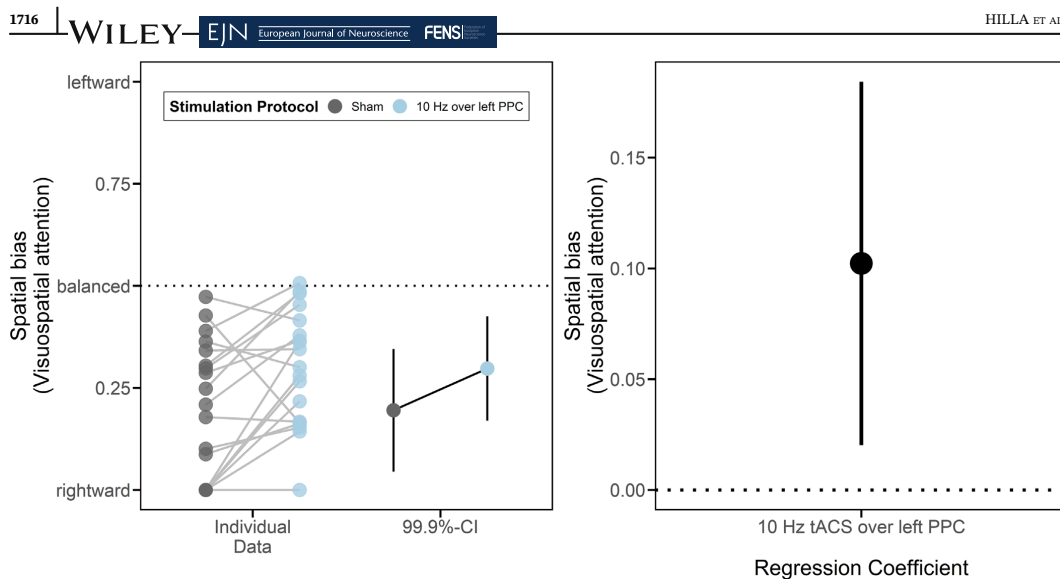


FIGURE 4 Effect of transcranial alternating current stimulation (tACS) at alpha frequency (10 Hz) on theory of visual attention *spatial bias* values. Values between 0 and .5 indicate a rightward, and between .5 and 1 a leftward *spatial bias*. Individuals' *spatial bias* values during sham stimulation served as baseline and are indicated as dark grey dots. Individuals' *spatial bias* values during alpha-tACS applied to the left posterior parietal cortex (PPC) are visualised as light blue dots. (left panel) Individuals' *spatial bias* values and corresponding 99.9%-confidence intervals. (right panel) Significant main effect of 10 Hz-tACS over left PPC: on average, individuals' *spatial bias* values were $< .5$ in the sham condition, and larger after 10 Hz-tACS had been applied over the left PPC in most of the individuals. Thus, alpha tACS to the left PPC seemed to have reduced most individuals' rightward *spatial bias* compared to baseline. The dot indicates the average, and whiskers the Benjamini–Hochberg-corrected confidence interval.

unlikely or just weakly modulated this association. Similar effects were found when grouped by *day*, see supporting information.

4 | DISCUSSION

The aim of this study was to demonstrate that modulating (right hemispheric **H4**) [Hung et al., 2005; Kraft et al., 2015; Moos et al., 2012]) posterior parietal alpha activity using tACS may affect individuals' speed of information processing (**H1**) (Hilla et al., 2020) and short-term memory capacity (**H3**) (Finke et al., 2005) by impacting on their attentional control functions (**H2**) (Bavelier & Green, 2019; Helfrich et al., 2014; Kemmerer et al., 2022; Riddle et al., 2020; Sauseng et al., 2009; Vogeti et al., 2022). However, the participants displayed similar speed of information processing and short-term memory capacity regardless of stimulation condition. In addition to that, alpha-tACS applied over individuals' *left* but not right PPC impacted on their visuospatial attention orientation. Thus, our data support **H2** but not **H1**, **H3** and **H4**.

4.1 | Inter-hemispheric competition and visuospatial attentional processing

We did not expect our participants to attend stronger to the right than the left visual field. In fact, previous research indicated that healthy individuals prevalently demonstrate a visuospatial bias towards the *left* and not the right visual field—a phenomenon established as *pseudoneglect* (Brooks et al., 2014). According to the *activation-orientation hypothesis* (AOH) such an attentional bias may be related to differential hemispheric activation with stronger biases emerging contralateral to the hemisphere with the higher excitation level (Reuter-Lorenz et al., 1990). Thus, *pseudoneglect* might be a consequence of higher excitation in the right as compared to the left hemisphere during visuospatial attentional processing (Siman-Tov et al., 2007). In line with this, Loftus and Nicholls (2012) showed that individuals exhibited a significant reduction in *pseudoneglect* after anodal (excitatory) transcranial direct current stimulation had been applied to the left PPC. The authors suggested that this effect might be related to inter-hemispheric competition where the imbalance in excitation levels between the

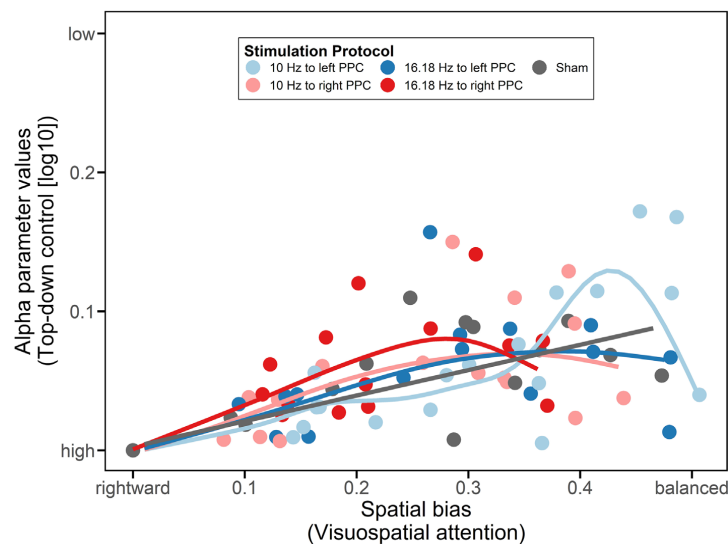


FIGURE 5 Association between theory of visual attention α (top-down control) and *spatial bias* values (visuospatial attention) in different brain stimulation conditions. α values close to zero indicate high top-down control and close to .30 no differentiation between targets and distractors. *Spatial bias* values $< .5$ suggest a rightward, and values $> .5$ a leftward spatial bias. Five different stimulation protocols were applied. Differential hemispheric stimulation is indicated by different colours (left hemispheric tACS: blue, right hemispheric tACS: red). Stimulation frequencies are indicated by different levels of luminance (10 Hz: bright, 16.18 Hz: dark). Sham stimulation is indicated by dark grey dots. Model fits were significant in each condition; and overall, there appeared to be (a tendency for) a linear association between the two variables in all conditions. PPC: posterior parietal cortex.

right and the left hemisphere might have been altered by anodal stimulation analogously shifting attention away from the left and more towards the right visual field.

Thus, the question of why participants in this study demonstrated nevertheless a *rightward* spatial bias needs to be addressed. One explanation for this may be an imbalance in alpha power between hemispheres. Alpha brain oscillatory activity is widely considered as a neural substrate of visuospatial attentional processing provided that lower/larger activity seems to coincide with processing states more/less favourable for information processing in line with the focus of attention, respectively (Jensen & Mazaheri, 2010; Klimesch, 2012; Peylo et al., 2021; Thut et al., 2006). Regarding the AOH (Reuter-Lorenz et al., 1990), one would then expect that attention would be biased towards a visual hemifield contralateral to the hemisphere with the lowest and ipsilateral to the hemisphere with the highest alpha oscillatory activity. Our data partially support this account given that alpha-tACS applied to the left PPC coincided with an attentional shift away from the right visual hemifield. But the question remains why our participants exhibited a rightward and not a leftward visuospatial bias in the sham condition in the first place? One explanation may

be that individuals might have demonstrated an increased alpha activity in the right as compared to the left hemisphere during visuospatial attentional processing. In support of this, Gallotto et al. (2020) found that individuals exhibited a larger alpha power in the right as compared to the left hemisphere in neutral conditions while performing a spatial orientation task. This implies that individuals may display an imbalance in hemispheric alpha activity even in conditions where attention is not cued towards one particular hemifield. Furthermore, individuals displayed larger differences in alpha activity between neutral and cued trials in the left as compared to the right hemisphere. This indicates that there may be a larger potential for alpha power modulation in the left than the right hemisphere. Thus, our participants' visuospatial attention bias towards the right visual field might have been driven by a larger alpha activity in the right hemisphere. Moreover, this effect may only have been altered by left hemispheric alpha-tACS application provided that there may have been a larger propensity for modulation in the left hemisphere. However, further research on alpha oscillatory activity during this task execution will be required to test these hypotheses.

4.2 | Association between TVA spatial bias and α values

Furthermore, we did not expect a significant relationship between TVA α and *spatial bias* values. This was because Wiegand et al. (2018) demonstrated that TVA visuospatial attentional processing and top-down control were related to distinct electrophysiological mechanisms which implied that these parameters were independent. In contrast, our findings suggest an association between these two parameters such that individuals' ability of target enhancement may be stronger if visuospatial attention was directed to the right visual field. One explanation for this may be that visuospatial attention may be deployed to facilitate target enhancement foremost in challenging conditions. In support of this, we observed that individuals displayed a larger error rate in response to targets presented in the left visual field as compared to the right one in particular if stimuli had been presented at the shortest exposure duration. But their performance was better in response to memory displays with targets only than targets and distractors irrespective of the remaining conditions. This indicates that visuospatial attention rather than target enhancement may be deployed to deal with challenging circumstances, for example, processing information presented at very short exposure duration. Moreover, Shalev et al. (2018) showed that individuals' TVA top-down control could be increased by directing visuospatial attention towards the right visual field using a lateralised sustained attention task.¹⁰ Thus, TVA *spatial bias* and α parameter values may indeed reflect distinct cognitive functions. Nevertheless, these might interact.

4.3 | Video gaming effects

If we had been able to demonstrate that modulating alpha activity using tACS impacted on TVA speed of information processing through alterations in attentional control functions, we would have been able to imitate an effect previously observed in video game players, that is, that video game players' faster visual information processing coincided with alpha amplitude modulation (Hilla et al., 2020). Furthermore, this effect would have provided indirect evidence in favour of alpha power modulation potentially representing a causal mechanism of this effect. In addition to that, we would have been able to infer to some extent which attention control function, for example, target enhancement and/or visuospatial

attention processing, may have contributed to the effect. On top of that, combined, these effects would have provided indirect evidence in favour of the hypothesis according to which video games may train individuals in learning to deploy attention control such that they may develop efficient cognitive strategies (Bavelier & Green, 2019).

However, we had only been able to show that modulating alpha activity using tACS impacted on individuals' visuospatial attention orientation. Thus, one might conclude from this effect that alpha power modulation might not represent a neural substrate of TVA speed of information processing. In addition to that, one might doubt if alpha power modulation indeed contributed to video game players' faster information processing (Hilla et al., 2020). We believe that such a conclusion may be premature given that we may not have been able to imitate the exact the same neural modulation as observed in video game players using tACS. This is because alpha-tACS rather increases brain oscillatory activity (Helfrich et al., 2014; Kemmerer et al., 2022). In contrast, video game players' faster speed of information processing correlated with alpha amplitude attenuation time-locked to memory display processing (Hilla et al., 2020). The issue here may be not so much that tACS increases brain oscillatory activity (because even opposite effects, that is, slower speed of information processing related to increased alpha activity, would have supported our hypotheses) but rather that alpha-tACS would have been required to alter alpha power modulation specifically related to memory display processing. Hung et al. (2005), for instance, showed that 10-Hz repetitive transcranial magnetic stimulation (rTMS) time-locked to memory displays applied over individuals' right hemispheric PPC altered their TVA top-down control. In this context, rTMS represents a non-invasive brain stimulation method employing a different mechanism to alter brain oscillatory activity as compared to tACS. Nevertheless, both methods appear to induce similar effects (Veniero et al., 2015). Thus, a temporally more precise application of (a different) brain stimulation at alpha frequency may be suitable to impact on TVA speed of information processing via altered TVA top-down control. But further research will be required to prove this hypothesis.

Besides speed of information processing, we expected alpha-tACS to impact on TVA short-term memory capacity K . We derived this hypothesis from the observation that short-term memory performance was related to alpha power modulation (Riddle et al., 2020; Sauseng et al., 2009) and TVA speed of information processing and short-term memory capacity commonly correlate (Finke et al., 2005). Moreover, video game players have been frequently shown to demonstrate enhanced

¹⁰However, this effect did only manifest as a result of high-frequency transcranial random-noise stimulation to both hemispheres.

short-term memory processing (Blacker & Curby, 2013; McDermott et al., 2014; Tanaka et al., 2013). Thus, if our results had been in line with our hypotheses (**H1** and **H2**), this may have indirectly implied that alpha power modulation may account for video gaming effects—therefore also for differential short-term memory processing in video game players (Blacker & Curby, 2013; McDermott et al., 2014; Tanaka et al., 2013). However, we had not been successful in establishing such a relationship. We speculate that one explanation for this may be that short-term memory processing may be stronger related to theta oscillatory activity around 5 Hz rather than alpha power (Lisman, 2010; Riddle et al., 2020; Sauseng et al., 2009). For instance, Jaušovec et al. (2014), Bender et al. (2019) and Wolinski et al. (2018) showed that individuals' short-term memory capacity could be increased by means of theta-tACS applied over their PPC. Furthermore, Kraft et al. (2015) found that individuals' TVA short-term memory capacity could be altered by applying 6-Hz rTMS time-locked to memory displays over individuals' right precuneus. Thus, TVA *K* parameter values may be more likely affected by modulating theta as compared to alpha activity. But further research will be required to establish this.

5 | CONCLUSION

The aim of this study was to demonstrate that modulating posterior parietal alpha activity using tACS may impact on individuals' speed of information processing by alternating their attentional control functions. If our results had been in line with this, we would have been able to imitate an effect previously observed in video game players, that is, that video game players' faster visual information processing coincided with alpha amplitude modulation (Hilla et al., 2020). Thus, this effect would have indirectly indicated that alpha power modulation might represent a neural substrate of video gaming effects. However, we only managed to change individuals' visuospatial attention orientation by applying tACS at alpha frequency over their left PPC. This indicates that mere alterations in visuospatial attention processing related to alpha oscillatory activity unlikely account for differential cognitive processing as observed in video game players.

AUTHOR CONTRIBUTIONS

Yannik Hilla: Conceptualisation; methodology; project administration; investigation; data curation; formal analysis; visualisation; software; writing—original draft preparation; writing—review and editing. **Fabian Link:** Investigation; data curation. **Paul Sauseng:**

Conceptualisation; funding acquisition; methodology; resources; supervision; validation; writing—review and editing.

ACKNOWLEDGEMENTS

We would like to thank our colleagues Anna Lena Biel, Elisabeth V.C. Friedrich, Charline Peylo and Jörg von Mankowski for their helpful advice to improve our project. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study will be openly available in a repository on Open Science Framework (<https://osf.io/rp2n6/>).

ETHICAL STATEMENT

Studies involving human participants were reviewed and approved by the local ethics review board. The participants provided their written informed consent to participate in this study.

ORCID

Yannik Hilla  <https://orcid.org/0000-0002-4870-7051>

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ejn.15968>.

REFERENCES

- Barton, K. (2020). *MuMin: Multi-model inference*. Retrieved from <https://CRAN.R-project.org/package=MuMin>
- Bavelier, D., Achtman, R. L., Mani, M., & Föcker, J. (2012). Neural bases of selective attention in action video game players. *Vision Research*, *61*, 132–143. <https://doi.org/10.1016/j.visres.2011.08.007>
- Bavelier, D., & Green, C. S. (2019). Enhancing attentional control: Lessons from action video games. *Neuron*, *104*(1), 147–163. <https://doi.org/10.1016/j.neuron.2019.09.031>
- Bavelier, D., Green, C. S., Pouget, A., & Schrater, P. (2012). Brain plasticity through the life span: Learning to learn and action video games. *Annual Review of Neuroscience*, *35*, 391–416. <https://doi.org/10.1146/annurev-neuro-060909-152832>
- Bediou, B., Adams, D. M., Mayer, R. E., Tipton, E., Green, C. S., & Bavelier, D. (2018). Correction: Meta-analysis of action video game impact on perceptual, attentional, and cognitive skills [psychological bulletin]. *Psychological Bulletin*, *144*(9), 978–979.
- Bejjanki, V. R., Zhang, R., Li, R., Pouget, A., Green, C. S., Lu, Z.-L., & Bavelier, D. (2014). Action video game play

- facilitates the development of better perceptual templates. *Proceedings of the National Academy of Sciences*, 111(47), 16961–16966. <https://doi.org/10.1073/pnas.1417056111>
- Bender, M., Romei, V., & Sauseng, P. (2019). Slow theta tACS of the right parietal cortex enhances contralateral visual working memory capacity. *Brain Topography*, 32(3), 477–481. <https://doi.org/10.1007/s10548-019-00702-2>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B: Methodological*, 57(1), 289–300.
- Blacker, K. J., & Curby, K. M. (2013). Enhanced visual short-term memory in action video game players. *Attention, Perception, & Psychophysics*, 75(6), 1128–1136. <https://doi.org/10.3758/s13414-013-0487-0>
- Blacker, K. J., Curby, K. M., Klobusicky, E., & Chein, J. M. (2014). Effects of action video game training on visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 40(5), 1992–2004. <https://doi.org/10.1037/a0037556>
- Brooks, J. L., Della Sala, S., & Darling, S. (2014). Representational pseudoneglect: A review. *Neuropsychology Review*, 24(2), 148–165. <https://doi.org/10.1007/s11065-013-9245-2>
- Bundesden, C., Vangkilde, S., & Petersen, A. (2015). Recent developments in a computational theory of visual attention (TVA). *Vision Research*, 116, 210–218. <https://doi.org/10.1016/j.visres.2014.11.005>
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33(2), 261–304. <https://doi.org/10.1177/0049124104268644>
- Cain, M. S., Landau, A. N., & Shimamura, A. P. (2012). Action video game experience reduces the cost of switching tasks. *Attention, Perception, & Psychophysics*, 74(4), 641–647. <https://doi.org/10.3758/s13414-012-0284-1>
- Campbell, J. I., & Thompson, V. A. (2012). MorePower 6.0 for ANOVA with relational confidence intervals and Bayesian analysis. *Behavior Research Methods*, 44(4), 1255–1265.
- Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal cortex controls spatial attention through modulation of anticipatory alpha rhythms. *Journal of Neuroscience*, 29(18), 5863–5872.
- Coretta, S. (2021). *Tidymv: Tidy model visualisation for generalised additive models*. Retrieved from <https://CRAN.R-project.org/package=tidymv>
- Dyrholm, M., Kyllingsbæk, S., Espeseth, T., & Bundesden, C. (2011). Generalizing parametric models by introducing trial-by-trial parameter variability: The case of TVA. *Journal of Mathematical Psychology*, 55(6), 416–429. <https://doi.org/10.1016/j.jmp.2011.08.005>
- Ester, M., Kriegel, H.-P., Sander, J., & Xu, X. (1996). A density-based algorithm for discovering clusters in large spatial databases with noise. *Kdd*, 96, 226–231.
- Finke, K., Bublak, P., Krummenacher, J., Kyllingsbæk, S., Müller, H. J., & Schneider, W. X. (2005). Usability of a theory of visual attention (TVA) for parameter-based measurement of attention i: Evidence from normal subjects. *Journal of the International Neuropsychological Society*, 11(7), 832–842. <https://doi.org/10.1017/S1355617705050976>
- Föcker, J., Cole, D., Beer, A. L., & Bavelier, D. (2018). Neural bases of enhanced attentional control: Lessons from action video game players. *Brain and Behavior: a Cognitive Neuroscience Perspective*, 8(7), e01019. <https://doi.org/10.1002/brb3.1019>
- Föcker, J., Mortazavi, M., Khoe, W., Hillyard, S. A., & Bavelier, D. (2019). Neural correlates of enhanced visual attentional control in action video game players: An event-related potential study. *Journal of Cognitive Neuroscience*, 31(3), 377–389. https://doi.org/10.1162/jocn_a_01230
- Gallotto, S., Duecker, F., Ten Oever, S., Schuhmann, T., De Graaf, T. A., & Sack, A. T. (2020). Relating alpha power modulations to competing visuospatial attention theories. *NeuroImage*, 207, 116429. <https://doi.org/10.1016/j.neuroimage.2019.116429>
- Green, C. S., & Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature*, 423(6939), 534–537. <https://doi.org/10.1038/nature01647>
- Green, C. S., Kattner, F., Eichenbaum, A., Bediou, B., Adams, D. M., Mayer, R. E., & Bavelier, D. (2017). Playing some video games but not others is related to cognitive abilities: A critique of Unsworth et al.(2015). *Psychological Science*, 28(5), 679–682.
- Green, C. S., Pouget, A., & Bavelier, D. (2010). Improved probabilistic inference as a general learning mechanism with action video games. *Current Biology*, 20(17), 1573–1579. <https://doi.org/10.1016/j.cub.2010.07.040>
- Green, C. S., Sugarman, M. A., Medford, K., Klobusicky, E., & Bavelier, D. (2012). The effect of action video game experience on task-switching. *Computers in Human Behavior*, 28(3), 984–994. <https://doi.org/10.1016/j.chb.2011.12.020>
- Hahsler, M., Piekenbrock, M., & Doran, D. (2019). Dbscan: Fast density-based clustering with R. *Journal of Statistical Software*, 91(1), 1–30. <https://doi.org/10.18637/jss.v091.i01>
- Helfrich, R. F., Schneider, T. R., Rach, S., Trautmann-Lengsfeld, S. A., Engel, A. K., & Herrmann, C. S. (2014). Entrainment of brain oscillations by transcranial alternating current stimulation. *Current Biology*, 24(3), 333–339. <https://doi.org/10.1016/j.cub.2013.12.041>
- Herrmann, C. S., Strüber, D., Helfrich, R. F., & Engel, A. K. (2016). EEG oscillations: From correlation to causality. *International Journal of Psychophysiology*, 103, 12–21.
- Hilla, Y., von Mankowski, J., Föcker, J., & Sauseng, P. (2020). Faster visual information processing in video gamers is associated with EEG alpha amplitude modulation. *Frontiers in Psychology*, 11, 3333.
- Hung, J., Driver, J., & Walsh, V. (2005). Visual selection and posterior parietal cortex: Effects of repetitive transcranial magnetic stimulation on partial report analyzed by Bundesden's theory of visual attention. *Journal of Neuroscience*, 25(42), 9602–9612. <https://doi.org/10.1523/JNEUROSCI.0879-05.2005>
- Jaušovec, N., Jaušovec, K., & Pahor, A. (2014). The influence of theta transcranial alternating current stimulation (tACS) on working memory storage and processing functions. *Acta Psychologica*, 146, 1–6. <https://doi.org/10.1016/j.actpsy.2013.11.011>
- Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: Gating by inhibition. *Frontiers in Human Neuroscience*, 4, 186. <https://doi.org/10.3389/fnhum.2010.00186>

- Kassambara, A. (2021). *Rstatix: Pipe-friendly framework for basic statistical tests*. Retrieved from <https://CRAN.R-project.org/package=rstatix>
- Kassambara, A., & Mundt, F. (2020). *Factoextra: Extract and visualize the results of multivariate data analyses*. Retrieved from <https://CRAN.R-project.org/package=factoextra>
- Kemmerer, S., Sack, A., de Graaf, T., Ten Oever, S., De Weerd, P., & Schuhmann, T. (2022). Frequency-specific transcranial neuromodulation of alpha power alters visuospatial attention performance. *Brain Research*, 1782, 147834. <https://doi.org/10.1016/j.brainres.2022.147834>
- Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, 16(12), 606–617. <https://doi.org/10.1016/j.tics.2012.10.007>
- Kraft, A., Dyrholm, M., Kehler, S., Kaufmann, C., Bruening, J., Kathmann, N., Bundesen, C., Irlbacher, K., & Brandt, S. A. (2015). TMS over the right precuneus reduces the bilateral field advantage in visual short term memory capacity. *Brain Stimulation*, 8(2), 216–223. <https://doi.org/10.1016/j.brs.2014.11.004>
- Krishnan, L., Kang, A., Sperling, G., & Srinivasan, R. (2013). Neural strategies for selective attention distinguish fast-action video game players. *Brain Topography*, 26(1), 83–97. <https://doi.org/10.1007/s10548-012-0232-3>
- Kyllingsbæk, S. (2006). Modeling visual attention. *Behavior Research Methods*, 38(1), 123–133. <https://doi.org/10.3758/BF03192757>
- Large, A. M., Bediou, B., Cekic, S., Hart, Y., Bavelier, D., & Green, C. S. (2019). Cognitive and behavioral correlates of achievement in a complex multi-player video game. *Media and Communication*, 7(4), 198–212. <https://doi.org/10.17645/mac.v7i4.2314>
- Li, R., Polat, U., Scalzo, F., & Bavelier, D. (2010). Reducing backward masking through action game training. *Journal of Vision*, 10(14), 1–13. <https://doi.org/10.1167/10.14.33>
- Lisman, J. (2010). Working memory: The importance of theta and gamma oscillations. *Current Biology*, 20(11), R490–R492. <https://doi.org/10.1016/j.cub.2010.04.011>
- Loftus, A. M., & Nicholls, M. E. (2012). Testing the activation-orientation account of spatial attentional asymmetries using transcranial direct current stimulation. *Neuropsychologia*, 50(11), 2573–2576. <https://doi.org/10.1016/j.neuropsychologia.2012.07.003>
- McDermott, A. F., Bavelier, D., & Green, C. S. (2014). Memory abilities in action video game players. *Computers in Human Behavior*, 34, 69–78. <https://doi.org/10.1016/j.chb.2014.01.018>
- Mishra, J., Zinni, M., Bavelier, D., & Hillyard, S. A. (2011). Neural basis of superior performance of action videogame players in an attention-demanding task. *Journal of Neuroscience*, 31(3), 992–998. <https://doi.org/10.1523/JNEUROSCI.4834-10.2011>
- Moliadze, V., Sierau, L., Lyzhko, E., Stenner, T., Werchowski, M., Siniatchkin, M., & Hartwigsen, G. (2019). After-effects of 10 Hz tACS over the prefrontal cortex on phonological word decisions. *Brain Stimulation*, 12(6), 1464–1474. <https://doi.org/10.1016/j.brs.2019.06.021>
- Moos, K., Vossel, S., Weidner, R., Sparing, R., & Fink, G. R. (2012). Modulation of top-down control of visual attention by cathodal tDCS over right IPS. *Journal of Neuroscience*, 32(46), 16360–16368. <https://doi.org/10.1523/JNEUROSCI.6233-11.2012>
- Neuwirth, E. (2014). *RColorBrewer: ColorBrewer palettes*. Retrieved from <https://CRAN.R-project.org/package=RColorBrewer>
- Pedersen, T. L. (2020). Patchwork: The composer of plots. Retrieved from <https://CRAN.R-project.org/package=patchwork>
- Perkins, D. N., & Salomon, G. (1992). Transfer of learning. In T. Husén & T. N. Postlethwaite (Eds.), *The international encyclopedia of education* (Vol. 2, pp. 425–441). Pergamon.
- Peylo, C., Hilla, Y., & Sauseng, P. (2021). Cause or consequence? Alpha oscillations in visuospatial attention. *Trends in Neurosciences*, 44(9), 705–713. <https://doi.org/10.1016/j.tins.2021.05.004>
- Pohl, C., Kunde, W., Ganz, T., Conzelmann, A., Pauli, P., & Kiesel, A. (2014). Gaming to see: Action video gaming is associated with enhanced processing of masked stimuli. *Frontiers in Psychology*, 5, 70. <https://doi.org/10.3389/fpsyg.2014.00070>
- R Core Team. (2022). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Reuter-Lorenz, P. A., Kinsbourne, M., & Moscovitch, M. (1990). Hemispheric control of spatial attention. *Brain and Cognition*, 12(2), 240–266.
- Riddle, J., Scimeca, J. M., Cellier, D., Dhanani, S., & D'Esposito, M. (2020). Causal evidence for a role of theta and alpha oscillations in the control of working memory. *Current Biology*, 30(9), 1748–1754. <https://doi.org/10.1016/j.cub.2020.02.065>
- Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., Glennon, M., Gerloff, C., Birbaumer, N., & Hummel, F. C. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology*, 19(21), 1846–1852. <https://doi.org/10.1016/j.cub.2009.08.062>
- Schenk, S., Lech, R. K., & Suchan, B. (2017). Games people play: How video games improve probabilistic learning. *Behavioural Brain Research*, 335, 208–214. <https://doi.org/10.1016/j.bbr.2017.08.027>
- Shalev, N., De Wandell, L., Dockree, P., Demeyere, N., & Chechlacz, M. (2018). Beyond time and space: The effect of a lateralized sustained attention task and brain stimulation on spatial and selective attention. *Cortex*, 107, 131–147. <https://doi.org/10.1016/j.cortex.2017.09.009>
- Siman-Tov, T., Mendelsohn, A., Schonberg, T., Avidan, G., Podlipsky, I., Pessoa, L., Gadoth, N., Ungerleider, L. G., & Hendler, T. (2007). Bihemispheric leftward bias in a visuospatial attention-related network. *Journal of Neuroscience*, 27(42), 11271–11278. <https://doi.org/10.1523/JNEUROSCI.0599-07.2007>
- Stoica, P., & Selen, Y. (2004). Model-order selection: A review of information criterion rules. *IEEE Signal Processing Magazine*, 21(4), 36–47. <https://doi.org/10.1109/MSP.2004.1311138>
- Strobach, T., Frensch, P. A., & Schubert, T. (2012). Video game practice optimizes executive control skills in dual-task and task switching situations. *Acta Psychologica*, 140(1), 13–24. <https://doi.org/10.1016/j.actpsy.2012.02.001>
- Tanaka, S., Ikeda, H., Kasahara, K., Kato, R., Tsubomi, H., Sugawara, S. K., Mori, M., Hanakawa, T., Sadato, N., Honda, M., & Watanabe, K. (2013). Larger right posterior parietal volume in action video game experts: A behavioral and

- voxel-based morphometry (VBM) study. *PLoS ONE*, 8(6), e66998. <https://doi.org/10.1371/journal.pone.0066998>
- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). α -band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, 26(37), 9494–9502. <https://doi.org/10.1523/JNEUROSCI.0875-06.2006>
- Veale, J. F. (2014). Edinburgh handedness inventory—short form: A revised version based on confirmatory factor analysis. *Laterality: Asymmetries of Body, Brain and Cognition*, 19(2), 164–177. <https://doi.org/10.1080/1357650X.2013.783045>
- Veniero, D., Vossen, A., Gross, J., & Thut, G. (2015). Lasting EEG/MEG aftereffects of rhythmic transcranial brain stimulation: Level of control over oscillatory network activity. *Frontiers in Cellular Neuroscience*, 9, 477. <https://doi.org/10.3389/fncel.2015.00477>
- Vogeti, S., Boetzel, C., & Herrmann, C. S. (2022). Entrainment and spike-timing dependent plasticity—A review of proposed mechanisms of transcranial alternating current stimulation. *Frontiers in Systems Neuroscience*, 16, 827353. <https://doi.org/10.3389/fnsys.2022.827353>
- Wagenmakers, E.-J. (2007). A practical solution to the pervasive problems of p values. *Psychonomic Bulletin & Review*, 14(5), 779–804. <https://doi.org/10.3758/BF03194105>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. Retrieved from <https://ggplot2.tidyverse.org>
- Wickham, H. (2021). *Tidy: Tidy messy data*. Retrieved from <https://CRAN.R-project.org/package=tidy>
- Wickham, H., François, R., Henry, L., & Müller, K. (2021). *Dplyr: A grammar of data manipulation*. Retrieved from <https://CRAN.R-project.org/package=dplyr>
- Wiegand, I., Napiórkowski, N., Töllner, T., Petersen, A., Habekost, T., Müller, H. J., & Finke, K. (2018). Event-related electroencephalographic lateralizations mark individual differences in spatial and nonspatial visual selection. *Journal of Cognitive Neuroscience*, 30(4), 482–497. https://doi.org/10.1162/jocn_a_01221
- Wolinski, N., Cooper, N. R., Sauseng, P., & Romei, V. (2018). The speed of parietal theta frequency drives visuospatial working memory capacity. *PLoS Biology*, 16(3), e2005348. <https://doi.org/10.1371/journal.pbio.2005348>
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 73(1), 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Wu, S., Cheng, C. K., Feng, J., D'angelo, L., Alain, C., & Spence, I. (2012). Playing a first-person shooter video game induces neuroplastic change. *Journal of Cognitive Neuroscience*, 24(6), 1286–1293. https://doi.org/10.1162/jocn_a_00192
- Zhu, H. (2021). *kableExtra: Construct complex table with 'kable' and pipe syntax*. Retrieved from <https://CRAN.R-project.org/package=kableExtra>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Hilla, Y., Link, F., & Sauseng, P. (2023). Alpha-tACS alters attentional control but not cognitive functions as video games do: A psychophysical investigation based on the theory of visual attention. *European Journal of Neuroscience*, 57(10), 1705–1722. <https://doi.org/10.1111/ejn.15968>

Running head: SUPPLEMENTARY MATERIAL

1

1 Supplementary Material: Alpha-tACS Alters Attentional Control but not Cognitive
2 Functions as Video Games Do: A Psychophysical Investigation based on the Theory of
3 Visual Attention

4 Yannik Hilla^{1,2,3}, Fabian Link¹, & Paul Sauseng¹

5 ¹ Ludwig-Maximilians-Universität

6 ² Universität der Bundeswehr München

7 ³ Graduate School of Systemic Neurosciences

8 Author Note

9 Ludwig-Maximilians-Universität (LMU), Department of Psychology, Leopoldstraße 13,
10 80802 Munich, Germany; Universität der Bundeswehr München, Allgemeine Psychologie,
11 Werner-Heisenberg-Weg 39, 85577 Neubiberg, Germany; Graduate School of Systemic
12 Neurosciences (LMU), Biozentrum, Großhaderner Straße 2, 82152 Planegg.

13 The work was conducted in a laboratory of the Department of Psychology at LMU.

14 Correspondence concerning this article should be addressed to Yannik Hilla,
15 Universität der Bundeswehr München, Allgemeine Psychologie, Werner-Heisenberg-Weg 39,
16 85577 Munich, Germany. E-mail: yannik.hilla@unibw.de

SUPPLEMENTARY MATERIAL

2

17 **Abbreviations**

- 18 • **AICc**: Second-Order Aikaike Information Criterion
- 19 • **AOH**: Activation-Orientation Hypothesis
- 20 • **BF₁₀**: Bayes Factor (in Support of H1)
- 21 • **BH**: Benjamini-Hochberg (Method)
- 22 • **BIC**: Bayesian Information Criterion
- 23 • **DBSCAN**: Density-Based Spatial Clustering of Applications with Noise
- 24 • **IAF**: Individual Alpha Frequency
- 25 • **PPC**: Posterior Parietal Cortex
- 26 • **rTMS**: repetitive Transcranial Magnetic Stimulation
- 27 • **tACS**: transcranial Alternating Current Stimulation
- 28 • **TVA**: Theory of Visual Attention

SUPPLEMENTARY MATERIAL

4

55 duration. This would have required approximately 3 hours, which was unreasonable to the
56 participants – especially, given that we applied *online* tACS stimulation. Instead, we
57 randomly and evenly paired exposure durations with memory displays. Thus, there were
58 slight differences between numbers of trials of each of the twelve conditions but the number
59 of trials across each level of *target position*, *trial type condition* and *exposure duration* was
60 balanced. This was sufficient for TVA computational modeling given that e.g., speed of
61 information processing is derived from the estimated number of memorized items per
62 exposure duration (short, medium and long) but not condition. On top of that, TVA spatial
63 bias was unlikely affected by this since spatial weights are derived from individuals' accuracy
64 in response to each location independent of condition. Also, TVA top-down control is
65 unlikely affected by this given that this parameter value is inferred from individuals'
66 differential performance in response to memory displays with targets only as compared to
67 targets and distractors independent of condition. However, at this point, one might also
68 wonder whether differential numbers of trials between *target position* and *trial type condition*
69 and *exposure duration* might affect TVA parameter estimation. In fact, previous research
70 indicated that TVA K , C and t_0 parameter estimation was more robust irrespective of small
71 or large numbers of trials than *spatial bias* and top-down control parameter estimation (Finke
72 et al., 2005). Thus, we decided to "relate more trials" to each level of *target position* and
73 *trial type condition* than *exposure duration* to achieve equally robust parameter estimates.

74 **Theory of Visual Attention Cognitive Functions**

75 **Differential Model Assumptions: balanced vs. biased visuospatial**
76 **attentional processing.** We used the following approach to choose which model estimates
77 should be used for further analyses: we investigated to which model assumption individuals'
78 performance fit best by using second-order Aikake information criterion ($AICc$) values of
79 each *model* (balanced vs. biased) by means of a hierarchical regression analysis allowing for
80 random intercepts for each individual. The smaller the $AICc$ value the better the model fit.

SUPPLEMENTARY MATERIAL

5

81 Then, we computed difference values between individuals' TVA parameter estimates and
82 sorted individuals into groups of over-estimation depending on whether *biased* estimates
83 were larger (balanced < biased) or smaller than *balanced* (balanced > biased) estimates. If
84 there were no differences in TVA parameter estimates between models, individuals' TVA
85 parameter value estimates of both models should remain at their relative order compared to
86 other individuals. In other words: there should be a linear relationship between TVA
87 parameter estimates of both models. However, if there were significant deviations between
88 these estimates, this may suggest that TVA parameter estimates might have been
89 over-estimated depending on the respective model assumption. Subsequently, we computed
90 hierarchical regression analyses with *absolute difference values* between TVA parameter
91 estimates of the two different models as criterion variable and *over-estimation* (balanced <
92 biased vs. balanced > biased) as categorical predictor variable with random intercepts for
93 each individual to quantify whether deviations were significant. Moreover, we contrasted the
94 amount of over-estimations (balanced < biased vs. balanced > biased) using binomial tests.

95 On average *AICc* values of the *biased* TVA model were between 172.65 and 221.59
96 values smaller than those of the *balanced* model. Thus, individuals' performances fit better
97 to the *biased* as compared to the *balanced* model. Moreover, *absolute difference values* of *K*
98 parameter estimates given an over-estimation in the *biased* model (balanced < biased) were
99 on average between 0.03 and 0.94 values larger than *absolute difference values* of *K*
100 parameter estimates given an over-estimation in the *balanced* model (balanced > biased).
101 Thus, the extent of over-estimation was significantly larger in the *biased* as compared to the
102 *balanced* model. Furthermore, *K* parameter estimates were on average between 1.81 to 1 and
103 4.85 to 1 times more often over-estimated in the *biased* as compared to the *balanced* model.
104 The latter was also the case for *C* parameter values where *C* parameter estimates had been
105 over-estimated on average between 1.16 to 1 and 2.82 to 1 times in the *biased* model relative
106 to the *balanced* one. The opposite seemed to be the case for α values given that on average α
107 estimates had been over-estimated between 1.09 to 1 and 2.64 to 1 times in the *balanced* as

SUPPLEMENTARY MATERIAL

6

108 compared to the *biased* model. But there appeared to be no significant effect in *absolute*
109 *difference values* of either C or α estimates given an over-estimation either in the *biased* or
110 *balanced* model. Also, there was no indication for significant differences in $t0$ parameter
111 estimates of either a *biased* or *balanced* TVA model.

112 **Brain Stimulation**

113 On average, human alpha activity peaks around 10 Hz. However, there are crucial
114 intra- and inter-individual differences in alpha activity depending on e.g., age, genetics,
115 hemispheric connectivity and cognitive processing (Başar, 2012; Haegens, Cousijn, Wallis,
116 Harrison, & Nobre, 2014; Smit, Wright, Hansell, Geffen, & Martin, 2006). Thus, individuals
117 display slightly different peaks in their alpha activity. This is referred to as *individual alpha*
118 *frequency* (IAF). Non-invasive brain stimulation applied at IAF is supposed to induce
119 stronger and more reliable effects than at mean peak frequency (Kasten, Duecker, Maack,
120 Meiser, & Herrmann, 2019; Vogeti, Boetzel, & Herrmann, 2022). In support of this,
121 Kemmerer and colleagues (2022) showed that tACS applied at IAF but not at IAF
122 plus/minus 2 Hz caused a visuospatial shift towards the left visual field relative to sham
123 condition. However, it should also be noted that these control stimulations might have been
124 inappropriate in some individuals given that their IAF ranged between 8 and 11.4 Hz and
125 thus likely smeared into other frequency bands, e.g., theta (ca. 5 Hz) and beta (ca. 13 Hz).
126 Moreover, Helfrich and colleagues (2014) found that tACS applied at 10 Hz and IAF over
127 the PPC caused similar stimulation effects. Thus, alpha-tACS applied at 10 Hz seems to be
128 equally sufficient to modulate alpha power as at IAF.

129

Results

130 Impact of all tACS Protocols on Spatial Bias Values

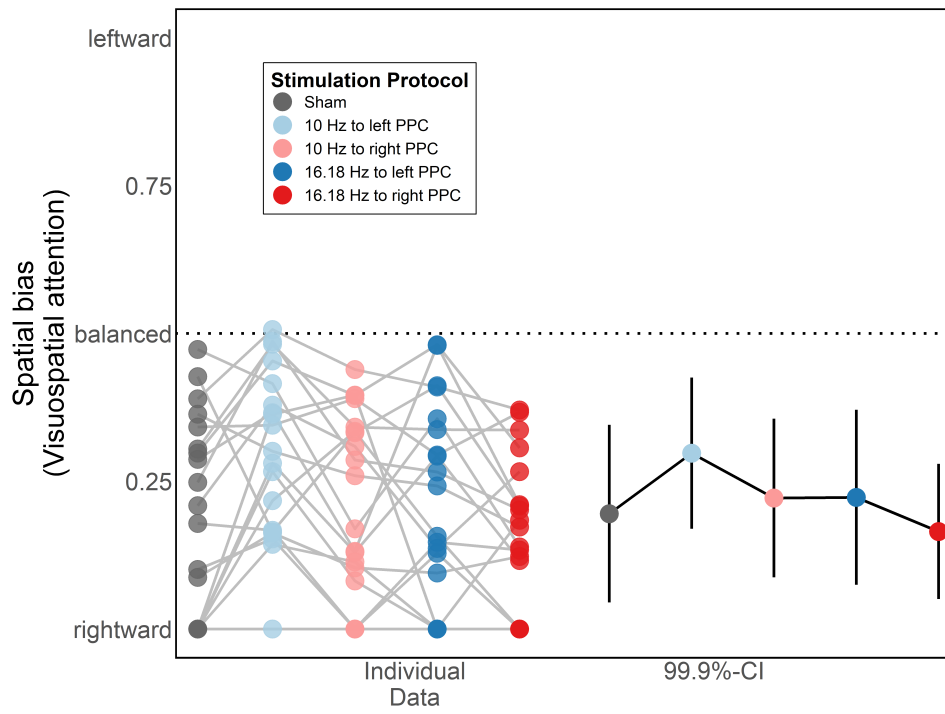


Figure 1. Effect of Transcranial Alternating Current Stimulation (tACS) on Theory of Visual Attention *Spatial Bias* Values. Values between 0 and 0.5 indicate a rightward, and between 0.5 and 1 a leftward *spatial bias*. TACS was delivered either at 10 Hz (bright) or 16.18 Hz (dark) over either the left (blue) or right (red) posterior parietal cortex (PPC). Individuals' *spatial bias* values during sham condition served as baseline and are indicated as dark gray dots. Left side: individuals' *spatial bias* values. Right side: corresponding 99.9 %-confidence intervals.

131 Associations between TVA Parameter Values

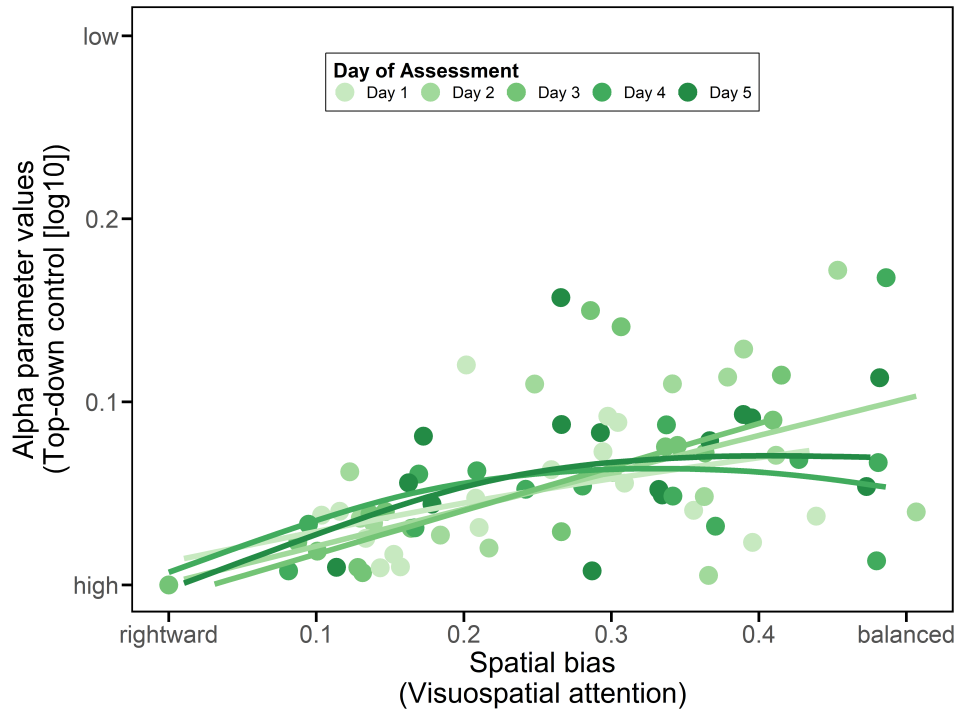


Figure 2. Association Between Theory of Visual Attention α (Top-Down Control) and *Spatial Bias* Values (Visuospatial Attention) on different days. α values close to zero indicate high top-down control and close to 0.30 no differentiation between targets and distractors. *Spatial bias* values < 0.5 suggest a rightward, and values > 0.5 a leftward spatial bias. There are data points from five different days. The order of days is indicated by different shades of green. Model fits were significant for each day ($\Delta AICc = 17.77$, $BF_{10} > 100$, $CI_{Gauss} = [0.00; 0.11]$, $range\ size_{Gauss} = 10.32\%$, $ps_{BH} < .011$). But fits were quite similar indicating that the relationship between TVA parameters did not differ between days.

References

- 132
133 Başar, E. (2012). A review of alpha activity in integrative brain function: Fundamental
134 physiology, sensory coding, cognition and pathology. *International Journal of*
135 *Psychophysiology*, *86*(1), 1–24.
- 136 Finke, K., Bublak, P., Krummenacher, J., Kyllingsbæk, S., Müller, H. J., & Schneider, W.
137 X. (2005). Usability of a theory of visual attention (TVA) for parameter-based
138 measurement of attention i: Evidence from normal subjects. *Journal of the International*
139 *Neuropsychological Society*, *11*(7), 832–842.
- 140 Haegens, S., Cousijn, H., Wallis, G., Harrison, P. J., & Nobre, A. C. (2014). Inter-and
141 intra-individual variability in alpha peak frequency. *Neuroimage*, *92*, 46–55.
- 142 Helfrich, R. F., Schneider, T. R., Rach, S., Trautmann-Lengsfeld, S. A., Engel, A. K., &
143 Herrmann, C. S. (2014). Entrainment of brain oscillations by transcranial alternating
144 current stimulation. *Current Biology*, *24*(3), 333–339.
- 145 Kasten, F. H., Duecker, K., Maack, M. C., Meiser, A., & Herrmann, C. S. (2019).
146 Integrating electric field modeling and neuroimaging to explain inter-individual
147 variability of tACS effects. *Nature Communications*, *10*(1), 1–11.
- 148 Kemmerer, S., Sack, A., Graaf, T. de, Ten Oever, S., De Weerd, P., & Schuhmann, T. (2022).
149 Frequency-specific transcranial neuromodulation of alpha power alters visuospatial
150 attention performance. *Brain Research*, *1782*, 147834.
- 151 Smit, C. M., Wright, M. J., Hansell, N. K., Geffen, G. M., & Martin, N. G. (2006). Genetic
152 variation of individual alpha frequency (IAF) and alpha power in a large adolescent twin
153 sample. *International Journal of Psychophysiology*, *61*(2), 235–243.
- 154 Vogeti, S., Boetzel, C., & Herrmann, C. S. (2022). Entrainment and spike-timing dependent
155 plasticity—a review of proposed mechanisms of transcranial alternating current
156 stimulation. *Frontiers in Systems Neuroscience*, *16*.

General Discussion

We found that video game players' speed of information processing improved in the course of performing a visual short-term memory task; and that this effect, in turn, correlated with an increase in EEG alpha amplitude attenuation (Hilla et al., 2020). In this regard, alpha oscillatory activity may represent a top-down control driven *gating* mechanism to modulate the likelihood of processing information (Peylo et al., 2021). This corresponds well with the ascribed role of attentional control functions in transfer effects associated with video gaming. Thus, video game players appear to acquire the ability of learning to develop effective cognitive and behavioral strategies by applying attentional control functions in order to enhance processing relevant and to suppress processing irrelevant information (Bavelier & Green, 2019).

But we were not able to show that individuals' speed of information processing (in addition to their visuospatial orientation) changed as a result of *transcranial alternating current stimulation* (tACS) applied at alpha frequency over the left posterior parietal cortex (Hilla et al., 2023). Thus, we had not been successful in our attempt of artificially inducing alterations in speed of information processing as observed in video game players by modulating non-video game players' alpha oscillatory activity using non-invasive brain stimulation (Hilla et al., 2020). Such an effect, however, would have been required to conclude that there was a causal relationship between alterations in alpha activity and transfer effects related to video gaming.

Thus, there appears to be inconclusive evidence both in favor and opposition of our thesis according to which alterations in alpha oscillatory activity may represent a neural substrate of transfer effects related to video gaming. On second thought, our results rather challenge the functional description of attentional control provided by Bavelier and Green (2019). This is because, they indicate that video game playing unlikely alters attentional control functions, such as selective and visuospatial attention, *per sé* but rather the algorithmic level thereof. We will discuss how a computational model based on the *theory of*

visual attention (TVA) (Bundesen, 1990; Bundesen, Vangkilde, & Petersen, 2015; Dyrholm, Kyllingsbæk, Espeseth, & Bundesen, 2011) may be used to operationalize this algorithmic level. In addition to that, we will elaborate how *gating* as operationalized by alpha oscillatory activity may be related to this model. Thus, we will argue that our results in fact mostly support our hypotheses.

A Computational Model of Attentional Control Based on the Theory of Visual Attention (TVA) to Operationalize Video Gaming Effects

Improved TVA Information Processing Capacity in Video Game Players Relates to Higher-Level Selective Attention Processing. There is no single cognitive function that reflects attentional control. In contrast, individuals display attentional control as a result of employing predominantly attention and executive cognitive functions (Bavelier & Green, 2019), e.g., sustained, selective and visuospatial attention (Chun, Golomb, Turk-Browne, et al., 2011), and top-down inhibition, switching/shifting and updating (Friedman & Miyake, 2017; Miyake et al., 2000). Given that video game players have been shown to exhibit superior performance in tasks requiring the application of these functions (Bediou et al., 2018b; Blacker et al., 2014; Föcker et al., 2018, 2019; Green & Bavelier, 2003; Strobach et al., 2012), and based on the observation that their superior performance appears to coincide with an improving signal-to-noise ratio (Bejjanki et al., 2014), it was proposed that altered attentional control might play a significant role in video gaming effects (Bavelier & Green, 2019). In this regard, attentional control is supposed to enable individuals to focus on processing relevant information while simultaneously being able to suppress irrelevant information (Bavelier & Green, 2019). However, an algorithmic solution to this computation has not yet been provided. Thus, the concept of attentional control is quite ambivalent. As a result, it has been challenging to infer which and how functional characteristics of attentional control differ between video game players and control individuals. To solve this issue, we used a computational model based on TVA (Bundesen, 1990; Bundesen et al., 2015;

Dyrholm et al., 2011).

TVA operationalizes attention processing based on the following assumptions (Bundesen, 1990; Bundesen et al., 2015): firstly, individuals' cognitive processing capacities are considered limited such that e.g., only a limited amount of information may be encoded and held in memory. Secondly, sensory information is processed in parallel. Thus, there is a race for information being encoded into memory. Thirdly, the likelihood of information being encoded depends on the interplay between two attention control functions, i.e., *pigeonholing* and *filtering* (Broadbent, 1970). *Pigeonholing* serves to prioritize object *categories*, e.g., color. *Filtering* allows to prioritize *features* of objects, e.g., red over blue. Thus, the conjunction between pigeonholing and filtering predominantly reflects an hierarchical selective attention mechanism. With reference to these assumptions, the *rate equation* was developed to model the likelihood of information being encoded into memory (1) (Bundesen, 1990; Bundesen et al., 2015; Dyrholm et al., 2011).

$$v_x(i) = \eta(x, i) \times \beta_i \times \frac{w_x}{\sum_{z \in S} w_z} \quad (1)$$

In this regard, $v_x(i)$ denotes the rate at which an object x may be classified as belonging to category i , and hence encoded into memory. $v_x(i)$ is computed as a function of the *sensory evidence*, $\eta(x, i)$, in favor of object x being classifiable as belonging to category i ; the *sensory decision bias*, β_i , in favor of processing objects of category i , and the weight, w_x , in favor of processing object x over other objects z in the visual field S . The magnitude of $\eta(x, i)$ depends on the resolution of the sensory information i related to x . For instance, $\eta(x, i)$ is small in the dark as individuals may simply not be able to perceive information under these circumstances. β_i refers to *pigeonholing*. Attentional weights are computed as described by the *weighting equation* (2),

$$w_x = \sum_{j \in G} \eta(x, j) \times \pi_j \quad (2)$$

where the weight of processing object x depends on the sum of the product between the

sensory evidence that object x has feature j and the pertinence weight, π_j , in favor of processing feature j in contrast to other features included in G . Thus, this weighting process reflects *filtering* (Bundesen, 1990; Bundesen et al., 2015; Dyrholm et al., 2011).

As a consequence, cognitive functions, such as short-term memory capacity, K , speed of information processing, C , encoding duration, t_0 , visuospatial attention processing, *spatial bias*, and top-down control, α , may be derived from individuals' recall accuracy of memorized information. In this regard, we and colleagues most reliably observed that video game players appear to display a superior information processing capacity as indicated by larger C values in comparison to control individuals (Hilla et al., 2020; Schubert et al., 2015; Wilms et al., 2013) (see also, **Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation in Research Projects**, for more details). But no differences in visuospatial attention or top-down control had been found. Such effects, however, would have been required to support the idea that improved attentional control accounted for gaming effects (Bavelier & Green, 2019).

Nevertheless, it might be premature to dismiss Bavelier and Green's account (2019) based on these results. The reason for this is, that the *rate equation* can be simplified as described in equation (3),

$$v_x(i) = C \times \frac{w_x}{\sum_{z \in S} w_z} \quad (3)$$

such that the rate of processing object x may be considered as a function of a fraction of individuals' overall processing capacities. Hereby, C is the product between the *sensory evidence* that x is an object of category i and the *perceptual decision bias*, β_i , which is supposed to reflect *pigeonholing*. Thus, video game players' larger C parameter values may indicate superior sensory encoding abilities (Hilla et al., 2020; Schubert et al., 2015; Wilms et al., 2013) driven by enhanced higher-level selective attention processing given that *pigeonholing* plays a considerable role in selective attention (Broadbent, 1970; Bundesen, 1990; Bundesen et al., 2015).

We argue that indeed differential *pigeonholing* rather than sensory information processing abilities may be associated with performance differences between video game players and control individuals. One reason for that is, that TVA constitutes that the computation of *sensory evidence* depends on the quality of physical properties of information, e.g., luminescence or color resolution (Bundesen, 1990; Bundesen et al., 2015). Therefore, *sensory evidence* computations should be unaffected by video gaming as per definition. Nevertheless, one could argue that this assumption was hardly valid given that some cognitive operation must be executed to encode sensory information. In this regard, there is evidence that early perceptual processing may be independent of attention processing, which would match with TVA's description of $\eta(x, i)$ (Di Russo, Martinez, & Hillyard, 2003). Thus, video game players' faster information processing might be related to alterations in early information processing. In opposition to this, firstly, there are reasonable arguments in favor of these early cognitive operations being nevertheless associated with attention processing (Qin, Wiens, Rauss, & Pourtois, 2022). In addition to that, conscious information processing (as is the case if individuals memorize and report information) likely requires attention deployment (Jennings, 2015; Marchetti, 2012; Van Boxtel, Tsuchiya, & Koch, 2010). Secondly, Föcker and colleagues (2018) found that video game players' superior performance was correlated with alterations in neural markers of perceptual processing associated with but not independent of attention processing. Thus, it seems fair to conclude that video game players' superior performance may be associated with altered selective attention as indicated by *pigeonholing* (but not *filtering*) as opposed to mere perceptual processing. Consequentially, alterations in TVA C parameter values might in fact support Bavelier and Green's account (2019)

Extending the TVA Computational Model by a Saliency Map Framework to Allow for Flexibility Despite Fixed Cognitive Capacities. With this being said, one should bear in mind that the theoretical assumptions of TVA (Bundesen, 1990; Bundesen et al., 2015) and the *learning to learn* hypothesis (Bavelier, Green, et al., 2012) are not entirely

compatible. This is because, the *learning to learn* hypothesis proposes that video game players outperform control individuals in tasks as a result of developing better cognitive strategies after having learned the statistical regularities of tasks and how to employ attentional control to efficiently execute these tasks (Bavelier & Green, 2019; Bavelier, Green, et al., 2012). This implies that individuals' processing capacities may change in the course of performing a paradigm. But this opposes TVA's assumption that individuals' information processing capacities are fixed (Bundesen, 1990; Bundesen et al., 2015).

We propose that extending TVA's computational model by the concept of the *saliency map* (Itti & Koch, 2001) might allow to reconcile TVA and the *learning to learn* hypothesis. The *saliency map* account suggests that individuals' attention is drawn towards information exhibiting the highest level of salience (Itti & Koch, 2001). In this regard, the degree of salience is a function of the contrast in features, such as color, intensity, orientation, motion, etc., between stimuli. Thus, the stimulus that differs the most from all other stimuli catches individuals' attention. Therefore, a red flower surrounded by green grass figuratively pops out. In contrast, it is more difficult to identify a red flower if it stands among other diversely colored plants. These phenomena have been investigated early on by means of feature- and conjunction search paradigms (Treisman & Gelade, 1980; Treisman & Sato, 1990). Neuronal receptive field properties, e.g., sensitivity for edges or orientations, appear to be at the heart of the computation of *saliency map* contrasts (Itti & Koch, 2001). Thus, the most salient stimulus appears so as a result of how specifically neurons are triggered by physical properties of that stimulus. These computations may be modulated by top-down attention processing by weighting certain features stronger than others (Krummenacher & Müller, 2012). In addition to that, more contemporary *saliency map* models propose a hierarchically organized structure differentiating between sensory modalities, dimensions and features (Liesefeld, Liesefeld, Pollmann, & Müller, 2018). Thus, contrast computations and attention weighting seem to take place within modalities, across dimensions, and across features and may possibly interact (Töllner, Gramann, Müller, & Eimer, 2009). TVA might allow an

algorithmic solution to these computations such that TVA's *sensory evidence* parameter may be equated with contrast computations as described in the *saliency map* approach.

Furthermore, top-down weighting could be modeled according to TVA's *sensory decision bias* (*pigeonholing*) and *weighting* (*filtering*) given that these highly resemble dimension- and feature-based weighting, respectively.

We argue that combining TVA and the *saliency map* framework provides a possible solution to the incompatibility between TVA and the *learning to learn* hypothesis in terms of assumptions of cognitive flexibility as the *saliency map* account allows to define individuals' scope of information processing without compromising an assumption of either one of these theories. This is because, as mentioned above, *saliency map* contrast computations are highly dependent on receptive field properties (Itti & Koch, 2001). Thus, neuronal activity may range within a certain scope depending on how specifically a stimulus may trigger a respective receptive field. But essentially there is an upper bound to this activity – at least due to the refractory period. Thus, *sensory evidence* may be constrained by individuals' neuronal firing properties. Following this logic, top-down attention processing may modulate neuronal firing rates within but not beyond this scope (Briggs, Mangun, & Usrey, 2013; McAdams & Maunsell, 1999; Moran & Desimone, 1985; Reynolds, Pasternak, & Desimone, 2000). Thus, an extension of the TVA computational model by the *saliency map* account allows alterations in TVA C parameter values as a result of changes in dimension-based weighting/*pigeonholing* associated with video gaming in line with the *learning to learn* hypothesis (Bavelier, Green, et al., 2012). But crucially it does not compromise TVA's assumption of fixed information processing capacity (Bundesen, 1990; Bundesen et al., 2015) provided that C was considered constrained by neuronal activity boundaries.

Alpha Oscillatory Activity as Neural Substrate of TVA Information

Processing. The theoretical framework described above is compatible with the neural interpretation of TVA (NTVA) (Bundesen, Habekost, & Kyllingsbæk, 2011). According to this account, *filtering* and *pigeonholing* correspond to modulations of the number and

activation level of neurons, respectively. Thus, *filtering* is associated with neuronal receptive fields being triggered by features j of objects x – changing neuronal states from baseline to active; and *pigeonholing* relates to top-down processing driven modulations of the activation level of these neurons such that processing information of category i receives a higher priority level compared to other categories. Dimension- and feature-based weighting may account for these neural operations. Thus, our extended TVA computational framework and the NTVA model are in line. Despite that, we do prefer an account according to which both dimension- and feature-based weighting predominantly impact on the neural activation level (as opposed to the number of active neurons) (Briggs et al., 2013; McAdams & Maunsell, 1999; Moran & Desimone, 1985; Reynolds et al., 2000). This is because, this approach allows for a continuum of neural activation in contrast to a switch between “baseline” and “active” states, which in our opinion, is a more ecologically valid model of neural firing rates. NTVA might nevertheless argue for differential effects of *filtering* and *pigeonholing* to ensure a fixed processing capacity. Thus, the magnitude of activation is constrained by the *pigeonholing* operation independent of the amount of active neurons (Bundesen et al., 2011). We account for this prerequisite by arguing that neuronal activity may be constrained in any case by neuronal firing properties. Thus, our framework is still compatible with and potentially more flexible than the NTVA model.

In this regard, we propose *gating* as operationalized by modulations of alpha oscillatory activity as a neural substrate of dimension-based weighting/*pigeonholing*. *Gating* refers to a mechanism to modulate the likelihood of information processing, and has been proposed based on the observation that high alpha power in the posterior parietal cortex coincided with a small likelihood of information being processed, while small alpha power correlated with a larger likelihood of information processing (Zhigalov & Jensen, 2020). This mechanism may be associated with the length of the duty cycle of alpha oscillatory activity. This is because, increased alpha amplitudes relate to shorter duty cycles and decreased amplitudes to longer duty cycles which, in turn, indicate the length of a time window for

information being able to transfer from early visual cortical areas to other brain areas for further processing (Peylo et al., 2021) (see, **Cause or Consequence? Alpha Oscillations in Visuospatial Attention in Research Projects**, for more details). Thus, *gating* represents a neural substrate of higher-level selective attention. In terms of our extended TVA framework, *gating* may serve to prioritize processing objects x of category i by providing information of category i a higher chance of being further processed than other categories. In this regard, one could consider alpha amplitude modulations as gates to either allow information to pass (attenuated amplitude \sim open door) or to prevent information from passing (high amplitude \sim closed door). Crucially, *gating* is compatible with (N)TVA's assumption of individuals' fixed information processing capacity as *gating* is constrained by alpha oscillatory activity. Thus, there may be inter- and intra-individual differences in frequency, amplitude and phase in alpha activity but these will manifest on average around 10 Hz and not exceed activity level boundaries due to neural firing properties (Başar, 2012; Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014; Smit, Wright, Hansell, Geffen, & Martin, 2006). Furthermore, *gating* is compatible with the idea of hierarchically organized processing stages as described in the *saliency map* approach (Itti & Koch, 2001) given that *gating* is likely employed at higher level processing stages after early perceptual processing (Antonov et al., 2020; Gundlach, Moratti, Forschack, & Müller, 2020; Zhigalov & Jensen, 2020). Thus, *gating* represents a promising neural substrate of higher-level selective attention potentially related to *pigeonholing* in our extended TVA framework.

One might argue now that our observation that individuals' C parameter values were unaffected by alpha-tACS (Hilla et al., 2023) might oppose this model since a modulation of alpha power should have impacted on individuals' selective attention processing (see, **Alpha-tACS Alters Attentional Control but not Cognitive Functions as Video Games Do in Research Projects**, for more details). However, this line of argumentation neglects to differentiate between *selective* and *visuospatial* attention processing. According to our framework, *gating* should serve to prioritize processing information of category i as

opposed to other categories. Therefore, prefrontal cortical areas were supposed to modulate alpha oscillatory activity such that there should be an attenuated alpha response to stimuli of category i (Peylo et al., 2021). In order to imitate this effect, our tACS protocol should have altered individuals' alpha oscillatory activity in a similar fashion. However, it is rather unlikely that we were able to achieve this given that tACS induces an overall increase in oscillatory activity (Helfrich et al., 2014; Kemmerer et al., 2022). Thus, alpha-tACS unlikely altered *pigeonholing* given that tACS increased alpha amplitudes in response to all categories. Visuospatial attention processing, on the other hand, could have been altered since tACS had been applied unilaterally over the posterior parietal cortex. Consequentially, an alpha-tACS induced hemispheric imbalance in alpha power may have re-oriented individuals' visuospatial attention as reflected by shifts of their TVA *spatial bias* (Hilla et al., 2023). Thus, our brain stimulation study results provide discriminatory evidence in favor of our extended TVA framework by emphasizing that indeed alterations in *selective* as opposed to *visuospatial* attention processing may account for video game players' enhanced speed of information processing.

Summary. By this point, we have elaborated that video game players' superior performance in (visual) short-term memory tasks were likely related to alterations in higher-level selective attention processing through changes in *pigeonholing* as reflected by larger TVA C parameter values (Hilla et al., 2020; Schubert et al., 2015; Wilms et al., 2013). In this regard, we provided a solution to the flexibility-fixed-capacity-incompatibility issue between TVA (Bundesen, 1990; Bundesen et al., 2015) and the *learning to learn* approach (Bavelier, Green, et al., 2012) by extending TVA's computational model (Dyrholm et al., 2011) by a *saliency map* framework (Itti & Koch, 2001). Moreover, we introduced *gating* as operationalized by alpha oscillatory activity (Gundlach et al., 2020; Zhigalov & Jensen, 2020) as neural mechanism of *pigeonholing* (Broadbent, 1970). Thus, we propose an extended computational model based on TVA to explain alterations in cognitive processing related to video gaming. In this regard, video game playing may train individuals in learning to process

rather relevant than irrelevant information by efficiently employing higher-level selective attention as operationalized by e.g., *pigeonholing* (Broadbent, 1970). This operation is supposed to be related to alpha amplitude modulation such that alpha power should attenuate in response to relevant information, e.g., category i , and potentially increase in response to irrelevant information. Note, however, that this mechanism should not be understood as a *gain control* mechanism such that relevant information processing was enhanced and irrelevant information processing suppressed. In contrast, we argue for a modulation of the likelihood of information processing in line with *gating* (Peylo et al., 2021; Zhigalov & Jensen, 2020).

Feasibility of the Extended TVA Model to Explain Video Gaming Effects.

Given that our framework does not rely on target information enhancement and distractor suppression mechanisms to operationalize attention control, it might provide new perspectives on controversial video gaming effects. For instance, we pointed out that it might be premature to interpret weaker neural responses in brain areas associated with top-down attention processing (even though correlated with superior performance in discrimination tasks) as indicative of enhanced attentional control in video game players (Bavelier, Achtman, et al., 2012; Föcker et al., 2018). In this regard, the authors (Bavelier, Achtman, et al., 2012; Föcker et al., 2018) argued in favor of superior attentional control with reference to the *neural efficiency hypothesis* (Haier et al., 1988). Thus, video game players might have been less challenged in performing the discrimination tasks as a result of their superior attention control, which correlated with weaker neural responses in brain areas related to top-down attention processing (Bavelier, Achtman, et al., 2012; Föcker et al., 2018). However, the *neural efficiency hypothesis* (Haier et al., 1988) is quite controversial. This is because, on the one hand, it appears to be supported by research on intelligence (Neubauer & Fink, 2009) and age-related cognitive decline (Rypma, Berger, Genova, Rebbechi, & D'Esposito, 2005). But at the same time, these effects are rather inconsistent because they are highly task-specific and appear to dependent on demographic variables (Dunst et al., 2014; Lipp et

al., 2012; Neubauer & Fink, 2009). Moreover, it is not compatible with neural correlates typically related to attention processing. Gazzaley, Cooney, McEvoy, Knight, and D'Esposito (2005), for instance, showed that individuals displayed larger neural responses to attended stimuli and weaker ones to ignored stimuli. Furthermore, Egner and Hirsch (2005) found that cognitive interference may be rather resolved by enhancing task-relevant processing as opposed to suppressing task-irrelevant information processing. Following this logic, one would have expected video game players to display enhanced target processing given that they performed better than control individuals; and this in turn, should have correlated with larger but not weaker brain activity while performing the tasks. In contrast, our framework would suggest that video game players might have been particularly selective in information processing. Thus, video game players appear to have applied a strategy to predominantly avoid information processing. This is because, alpha power has been often observed to be negatively correlated with blood-oxygenation-level-dependent signals (Pang & Robinson, 2018). Consequentially, video game players' weaker brain responses likely coincided with high alpha activity, which indicates a larger selectivity for information processing according to our framework. This implies that video game players in fact displayed enhanced attention processing, which is in line with Bavelier and Green's account (Bavelier & Green, 2019). Besides that, we have already elaborated that Wilms and colleagues (2013) and Schubert and colleague's (2015) results could be interpreted as in favor instead of opposition of Bavelier and Green's approach (Bavelier & Green, 2019). This is because, video game players' larger C parameter values are likely related to enhanced higher-level selective attention processing as operationalized by *pigeonholing* (Broadbent, 1970). However, our framework cannot explain why there were inconsistent results regarding SSVEPs in response to distractor stimuli in video game players (Krishnan et al., 2013; Mishra et al., 2011). This is because, SSVEPs are likely independent of alpha oscillatory activity (Antonov et al., 2020; Gundlach et al., 2020; Keitel et al., 2019). Hence, this effect is out of the scope of our framework.

Future Research

Future research will have to test whether *gating* as operationalized by alpha oscillatory activity may indeed provide a neural correlate of dimension-based weighting such that differential category weighting correlates with differential alpha amplitude modulation. In support of this, Snyder and Foxe (2010), for instance, found that individuals' alpha power was modulated in line with dimension-weighting such that alpha power increased in response to irrelevant categories as compared to relevant ones. Crucially, this modulation appears to apply in particular to later dimension-based as opposed to early feature-based selective attention processing (Gundlach, Forschack, & Müller, 2023; van Diepen, Miller, Mazaheri, & Geng, 2016; Wildegger, van Ede, Woolrich, Gillebert, & Nobre, 2017). Besides that, Freunberger, Klimesch, Griesmayr, Sauseng, and Gruber (2008) found that object recognition correlated with alpha amplitude modulation. This observation had a strong impact on the development of the *knowledge system* hypothesis according to which alpha power modulation was supposed to represent a mechanism of encoding based on long-term memory representations (Klimesch, 2012; Klimesch et al., 2011). Thus, there is essential evidence in favor of alpha power modulation representing a neural mechanism of higher-level selective attention at later processing stages in line with our framework but further research will be required to establish this processing hierarchy.

Besides that, future research will have to extend our framework by algorithmic solutions to cognitive operations preceding and following information encoding. TVA only proposes that the conjunction between *pigeonholing* and *filtering* modulates the likelihood of information processing during encoding (Bundesen, 1990; Bundesen et al., 2015). But it does not commit to any additional model assumption in terms of attention processing. Nevertheless, there are indications that individuals may employ attention in anticipation to stimulus processing, after stimulus processing and even in response to retro-cues – operations which also have been shown to correlate with alpha power modulation, respectively (Klimesch et al., 2011; Nenert, Viswanathan, Dubuc, & Visscher, 2012; Roesner, Arnau,

Skiba, Wascher, & Schneider, 2020; Spaak, Fonken, Jensen, & Lange, 2016; Worden et al., 2000). Thus, further research will be required to investigate whether our framework may only account for encoding or may also incorporate additional attention operations.

Furthermore, the concept of a quantitative representation of information in memory has been challenged. Schurgin, Wixted, and Brady (2020), for instance, provided strong evidence that individuals' memory recall may be operationalized by an encoding operation where the internal representation of memorized information is executed by means of a familiarity function. Thus, when individuals are asked to indicate which feature j of category i matches with a (memorized) target object x , the strength of the association between feature j of the probe and of the memorized object x appears to determine the memory recall accuracy. Thus, information is unlikely represented as quantifiable unit in memory but rather as a reversed *saliency map*. However, how external and internal encoding mechanisms interact and whether our framework may account for them remains an open question and requires further investigation.

In this regard, research on the functional role of interactions between prefrontal activity and posterior alpha oscillatory activity may be particularly interesting. This is because, there are indications that prefrontal areas control attention processing related to posterior parietal alpha activity (Capotosto et al., 2009; Sauseng, Feldheim, Freunberger, & Hummel, 2011) – however, whether this applies foremost to visuospatial attention orienting or also to additional attention operations remains an open question. Moreover, rather frontal theta activity around 5 Hz as opposed to posterior alpha power appears to be associated with information prioritization (Riddle, Scimeca, Cellier, Dhanani, & D'Esposito, 2020). Thus, alpha power might in fact only represent a size-variable *gate* to either allow for information to pass or not. But the central mechanism thereof may be controlled by frontal activity. If such a mechanism indeed existed, this would imply that alpha power modulation was just a means to filter information while the actual weighting operation might have taken place in prefrontal areas and earlier on. As a result, alpha oscillatory activity might still represent a

neural correlate of video gaming effects. However, alpha power modulation would represent rather an intermediate step within a complex weighting mechanism. Thus future research will be required to determine the significance of alpha power modulations in video gaming effects.

Conclusion

With all this being said and done, is it fair to conclude that alpha activity represents an essential neural substrate of transfer effects related to video gaming? Our experimental results mostly support this idea. This is because, we were able to demonstrate, firstly, that video game players may develop superior speed of information processing as function of time on task. Secondly, that this effect was likely relate to altered higher-level selective attention processing; and thirdly, that this effect coincided with an increase in alpha amplitude attenuation (Hilla et al., 2020). Thus, we were able to relate alterations in alpha oscillatory activity to a video gaming transfer effect in line with the *learning to learn* hypothesis (Bavelier & Green, 2019; Bavelier, Green, et al., 2012). Furthermore, our brain stimulation study results emphasize that this effect indeed likely required higher-level selective attention processing given that mere alterations in visuospatial attention processing had been insufficient to imitate the effect (Hilla et al., 2023).

References (General Introduction and Discussion)

- Aarseth, E., Bean, A. M., Boonen, H., Colder Carras, M., Coulson, M., Das, D., . . . van Rooji, A. (2017). Scholars' open debate paper on the world health organization ICD-11 gaming disorder proposal. *Journal of Behavioral Addictions, 6*(3), 267–270.
- Achtman, R. L., Green, C. S., & Bavelier, D. (2008). Video games as a tool to train visual skills. *Restorative Neurology and Neuroscience, 26*(4-5), 435–446.
- Anguera, J. A., Boccanfuso, J., Rintoul, J. L., Al-Hashimi, O., Faraji, F., Janowich, J., . . . Gazzaley, A. (2013). Video game training enhances cognitive control in older adults. *Nature, 501*(7465), 97–101.
- Antonov, P. A., Chakravarthi, R., & Andersen, S. K. (2020). Too little, too late, and in the wrong place: Alpha band activity does not reflect an active mechanism of selective attention. *Neuroimage, 219*, 117006.
- Başar, E. (2012). A review of alpha activity in integrative brain function: Fundamental physiology, sensory coding, cognition and pathology. *International Journal of Psychophysiology, 86*(1), 1–24.
- Bavelier, D., Achtman, R. L., Mani, M., & Föcker, J. (2012). Neural bases of selective attention in action video game players. *Vision Research, 61*, 132–143.
- Bavelier, D., & Green, C. S. (2019). Enhancing attentional control: Lessons from action video games. *Neuron, 104*(1), 147–163.
- Bavelier, D., Green, C. S., Pouget, A., & Schrater, P. (2012). Brain plasticity through the life span: Learning to learn and action video games. *Annual Review of Neuroscience, 35*, 391–416.
- Bediou, B., Adams, D. M., Mayer, R. E., Tipton, E., Green, C. S., & Bavelier, D. (2018a). Correction: Meta-analysis of action video game impact on perceptual, attentional, and cognitive skills [psychological bulletin, 144, 1, (2018), (77-110)]. *Psychological Bulletin, 144*(9), 978–979.
- Bediou, B., Adams, D. M., Mayer, R. E., Tipton, E., Green, C. S., & Bavelier, D. (2018b).

- Meta-analysis of action video game impact on perceptual, attentional, and cognitive skills. *Psychological Bulletin*, *144*(1), 77.
- Bejjanki, V. R., Zhang, R., Li, R., Pouget, A., Green, C. S., Lu, Z.-L., & Bavelier, D. (2014). Action video game play facilitates the development of better perceptual templates. *Proceedings of the National Academy of Sciences*, *111*(47), 16961–16966.
- Blacker, K. J., & Curby, K. M. (2013). Enhanced visual short-term memory in action video game players. *Attention, Perception, & Psychophysics*, *75*(6), 1128–1136.
- Blacker, K. J., Curby, K. M., Klobusicky, E., & Chein, J. M. (2014). Effects of action video game training on visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *40*(5), 1992–2004.
- Bonus, J. A., Peebles, A., & Riddle, K. (2015). The influence of violent video game enjoyment on hostile attributions. *Computers in Human Behavior*, *52*, 472–483.
- Boot, W. R., Kramer, A. F., Simons, D. J., Fabiani, M., & Gratton, G. (2008). The effects of video game playing on attention, memory, and executive control. *Acta Psychologica*, *129*(3), 387–398.
- Briggs, F., Mangun, G. R., & Usrey, W. M. (2013). Attention enhances synaptic efficacy and the signal-to-noise ratio in neural circuits. *Nature*, *499*(7459), 476–480.
- Broadbent, D. E. (1970). Stimulus set and response set: Two kinds of selective attention. In D. Mostofsky (Ed.), *Attention: Contemporary theory and analysis* (pp. 51–60). New York: New York, NY: Appleton- Century Crofts.
- Bundesen, C. (1990). A theory of visual attention. *Psychological Review*, *97*(4), 523–547.
- Bundesen, C., Habekost, T., & Kyllingsbæk, S. (2011). A neural theory of visual attention and short-term memory (NTVA). *Neuropsychologia*, *49*(6), 1446–1457.
- Bundesen, C., Vangkilde, S., & Petersen, A. (2015). Recent developments in a computational theory of visual attention (TVA). *Vision Research*, *116*, 210–218.
- Cain, M. S., Landau, A. N., & Shimamura, A. P. (2012). Action video game experience reduces the cost of switching tasks. *Attention, Perception, & Psychophysics*, *74*(4),

641–647.

- Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal cortex controls spatial attention through modulation of anticipatory alpha rhythms. *Journal of Neuroscience*, *29*(18), 5863–5872.
- Chiappe, D., Conger, M., Liao, J., Caldwell, J. L., & Vu, K.-P. L. (2013). Improving multi-tasking ability through action videogames. *Applied Ergonomics*, *44*(2), 278–284.
- Chun, M. M., Golomb, J. D., Turk-Browne, N. B., et al. (2011). A taxonomy of external and internal attention. *Annual Review of Psychology*, *62*(1), 73–101.
- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron*, *58*(3), 306–324.
- Cunningham, S., Engelstätter, B., & Ward, M. R. (2016). Violent video games and violent crime. *Southern Economic Journal*, *82*(4), 1247–1265.
- Deroy, O., Spence, C., & Noppeney, U. (2016). Metacognition in multisensory perception. *Trends in Cognitive Sciences*, *20*(10), 736–747.
- Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex*, *13*(5), 486–499.
- Dittmayer, M. (2014). *Stigma-videospiele. Hintergründe und verlauf der diskussion über gewaltdarstellende videospiele in deutschland*. Retrieved from <http://stigma-videospiele.de/>
- Dunst, B., Benedek, M., Jauk, E., Bergner, S., Koschutnig, K., Sommer, M., . . . Neubauer, A. (2014). Neural efficiency as a function of task demands. *Intelligence*, *42*, 22–30.
- Dyrholm, M., Kyllingsbæk, S., Espeseth, T., & Bundesen, C. (2011). Generalizing parametric models by introducing trial-by-trial parameter variability: The case of TVA. *Journal of Mathematical Psychology*, *55*(6), 416–429.
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature Neuroscience*, *8*(12), 1784–1790.
- Entertainment Software Association. (2022). *Essential facts about the video gaming industry*.

Retrieved from <https://www.theesa.com/wp-content/uploads/2022/06/2022-Essential-Facts-About-the-Video-Game-Industry.pdf>

- Ferguson, C. J., Copenhaver, A., & Markey, P. (2020). Reexamining the findings of the american psychological association's 2015 task force on violent media: A meta-analysis. *Perspectives on Psychological Science, 15*(6), 1423–1443.
- Ferguson, C. J., Olson, C. K., Kutner, L. A., & Warner, D. E. (2014). Violent video games, catharsis seeking, bullying, and delinquency: A multivariate analysis of effects. *Crime & Delinquency, 60*(5), 764–784.
- Föcker, J., Cole, D., Beer, A. L., & Bavelier, D. (2018). Neural bases of enhanced attentional control: Lessons from action video game players. *Brain and Behavior, 8*(7), e01019.
- Föcker, J., Mortazavi, M., Khoe, W., Hillyard, S. A., & Bavelier, D. (2019). Neural correlates of enhanced visual attentional control in action video game players: An event-related potential study. *Journal of Cognitive Neuroscience, 31*(3), 377–389.
- Foss, A. J. (2017). Use of video games for the treatment of amblyopia. *Current Opinion in Ophthalmology, 28*(3), 276–281.
- Freunberger, R., Klimesch, W., Griesmayr, B., Sauseng, P., & Gruber, W. (2008). Alpha phase coupling reflects object recognition. *Neuroimage, 42*(2), 928–935.
- Friedman, N. P., & Miyake, A. (2017). Unity and diversity of executive functions: Individual differences as a window on cognitive structure. *Cortex, 86*, 186–204.
- Furuya-Kanamori, L., & Doi, S. A. (2016). Angry birds, angry children, and angry meta-analysts: A reanalysis. *Perspectives on Psychological Science, 11*(3), 408–414.
- Gambacorta, C., Nahum, M., Vedamurthy, I., Bayliss, J., Jordan, J., Bavelier, D., & Levi, D. M. (2018). An action video game for the treatment of amblyopia in children: A feasibility study. *Vision Research, 148*, 1–14.
- Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down enhancement and suppression of the magnitude and speed of neural activity. *Journal of Cognitive Neuroscience, 17*(3), 507–517.

- Gopher, D., Well, M., & Bareket, T. (1994). Transfer of skill from a computer game trainer to flight. *Human Factors*, *36*(3), 387–405.
- Green, C. S., & Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature*, *423*(6939), 534–537.
- Green, C. S., & Bavelier, D. (2012). Learning, attentional control, and action video games. *Current Biology*, *22*(6), R197–R206.
- Green, C. S., Pouget, A., & Bavelier, D. (2010). Improved probabilistic inference as a general learning mechanism with action video games. *Current Biology*, *20*(17), 1573–1579.
- Greitemeyer, T. (2022). The dark and bright side of video game consumption: Effects of violent and prosocial video games. *Current Opinion in Psychology*, 101326.
- Gundlach, C., Forschack, N., & Müller, M. M. (2023). Global attentional selection of visual features is not associated with selective modulation of posterior alpha-band activity. *Psychophysiology*, (e14244), 1–12.
- Gundlach, C., Moratti, S., Forschack, N., & Müller, M. (2020). Spatial attentional selection modulates early visual stimulus processing independently of visual alpha modulations. *Cerebral Cortex*, *30*(6), 3686–3703.
- Haegens, S., Cousijn, H., Wallis, G., Harrison, P. J., & Nobre, A. C. (2014). Inter- and intra-individual variability in alpha peak frequency. *Neuroimage*, *92*, 46–55.
- Haier, R. J., Siegel Jr, B. V., Nuechterlein, K. H., Hazlett, E., Wu, J. C., Paek, J., . . . Buchsbaum, M. S. (1988). Cortical glucose metabolic rate correlates of abstract reasoning and attention studied with positron emission tomography. *Intelligence*, *12*(2), 199–217.
- Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of alpha oscillations in temporal attention. *Brain Research Reviews*, *67*(1-2), 331–343.
- Hazarika, J., & Dasgupta, R. (2020). Neural correlates of action video game experience in a visuospatial working memory task. *Neural Computing and Applications*, *32*(8), 3431–3440.
- Hazarika, J., Kant, P., Dasgupta, R., & Laskar, S. H. (2018). Neural modulation in action

- video game players during inhibitory control function: An EEG study using discrete wavelet transform. *Biomedical Signal Processing and Control*, *45*, 144–150.
- Helfrich, R. F., Schneider, T. R., Rach, S., Trautmann-Lengsfeld, S. A., Engel, A. K., & Herrmann, C. S. (2014). Entrainment of brain oscillations by transcranial alternating current stimulation. *Current Biology*, *24*(3), 333–339.
- Hilgard, J., Sala, G., Boot, W. R., & Simons, D. J. (2019). Overestimation of action-game training effects: Publication bias and salami slicing. *Collabra: Psychology*, *5*(1), 30.
- Hilla, Y., Link, F., & Sauseng, P. (2023). Alpha-tACS alters attentional control but not cognitive functions as video games do: A psychophysical investigation based on the theory of visual attention. *European Journal of Neuroscience*, *57*(10), 1705–1722.
- Hilla, Y., Von Mankowski, J., Föcker, J., & Sauseng, P. (2020). Faster visual information processing in video gamers is associated with EEG alpha amplitude modulation. *Frontiers in Psychology*, *11*, 599788.
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, *2*(3), 194–203.
- Jennings, C. D. (2015). Consciousness without attention. *Journal of the American Philosophical Association*, *1*(2), 276–295.
- Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: Gating by inhibition. *Frontiers in Human Neuroscience*, *4*, 186.
- Keitel, C., Keitel, A., Benwell, C. S., Daube, C., Thut, G., & Gross, J. (2019). Stimulus-driven brain rhythms within the alpha band: The attentional-modulation conundrum. *Journal of Neuroscience*, *39*(16), 3119–3129.
- Kemmerer, S., Sack, A., Graaf, T. de, Ten Oever, S., De Weerd, P., & Schuhmann, T. (2022). Frequency-specific transcranial neuromodulation of alpha power alters visuospatial attention performance. *Brain Research*, *1782*, 147834.
- Kersten, R., & Greitemeyer, T. (2022). Why do habitual violent video game players believe in the cathartic effects of violent video games? A misinterpretation of mood improvement

- as a reduction in aggressive feelings. *Aggressive Behavior*, 48(2), 219–231.
- Kim, H. S., Son, G., Roh, E.-B., Ahn, W.-Y., Kim, J., Shin, S.-H., . . . Choi, K.-H. (2022). Prevalence of gaming disorder: A meta-analysis. *Addictive Behaviors*, 126, 107183.
- Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, 16(12), 606–617.
- Klimesch, W., Fellinger, R., & Freunberger, R. (2011). Alpha oscillations and early stages of visual encoding. *Frontiers in Psychology*, 2, 118.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews*, 53(1), 63–88.
- Koepp, M. J., Gunn, R. N., Lawrence, A. D., Cunningham, V. J., Dagher, A., Jones, T., . . . Grasby, P. (1998). Evidence for striatal dopamine release during a video game. *Nature*, 393, 266–268.
- Kollins, S. H., DeLoss, D. J., Cañadas, E., Lutz, J., Findling, R. L., Keefe, R. S., . . . Faraone, S. V. (2020). A novel digital intervention for actively reducing severity of paediatric ADHD (STARS-ADHD): A randomised controlled trial. *The Lancet Digital Health*, 2(4), e168–e178.
- Krishnan, L., Kang, A., Sperling, G., & Srinivasan, R. (2013). Neural strategies for selective attention distinguish fast-action video game players. *Brain Topography*, 26(1), 83–97.
- Krummenacher, J., & Müller, H. J. (2012). Dynamic weighting of feature dimensions in visual search: Behavioral and psychophysiological evidence. *Frontiers in Psychology*, 3, 221.
- Kühn, S., Romanowski, A., Schilling, C., Lorenz, R., Mörsen, C., Seiferth, N., . . . The IMAGEN Consortium. (2011). The neural basis of video gaming. *Translational Psychiatry*, 1(11), e53–e53.
- Large, A. M., Bediou, B., Cekic, S., Hart, Y., Bavelier, D., & Green, C. S. (2019). Cognitive and behavioral correlates of achievement in a complex multi-player video game. *Media and Communication*, 7(4), 198–212.

- Lee, E.-J., Kim, H. S., & Choi, S. (2021). Violent video games and aggression: Stimulation or catharsis or both? *Cyberpsychology, Behavior, and Social Networking*, *24*(1), 41–47.
- Li, R. W., Ngo, C., Nguyen, J., & Levi, D. M. (2011). Video-game play induces plasticity in the visual system of adults with amblyopia. *PLoS Biology*, *9*(8), e1001135.
- Li, R., Polat, U., Scalzo, F., & Bavelier, D. (2010). Reducing backward masking through action game training. *Journal of Vision*, *10*(14), 33–33.
- Liesefeld, H. R., Liesefeld, A. M., Pollmann, S., & Müller, H. J. (2018). Biasing allocations of attention via selective weighting of saliency signals: Behavioral and neuroimaging evidence for the dimension-weighting account. *Processes of Visuospatial Attention and Working Memory*, 87–113.
- Lipp, I., Benedek, M., Fink, A., Koschutnig, K., Reishofer, G., Bergner, S., . . . Neubauer, A. (2012). Investigating neural efficiency in the visuo-spatial domain: An fMRI study. *PLoS One*, *7*(12), e51316.
- Lu, T., Tang, M., Guo, Y., Zhou, C., Zhao, Q., & You, X. (2022). Effect of video game experience on the simulated flight task: The role of attention and spatial orientation. *Australian Journal of Psychology*, *74*(1), 1–18.
- Lynch, J., Aughwane, P., & Hammond, T. M. (2010). Video games and surgical ability: A literature review. *Journal of Surgical Education*, *67*(3), 184–189.
- Marchetti, G. (2012). Against the view that consciousness and attention are fully dissociable. *Frontiers in Psychology*, *3*, 36.
- Markey, P. M., Ivory, J. D., Slotter, E. B., Oliver, M. B., & Maglalang, O. (2020). He does not look like video games made him do it: Racial stereotypes and school shootings. *Psychology of Popular Media*, *9*(4), 493–498.
- Markey, P. M., Markey, C. N., & French, J. E. (2015). Violent video games and real-world violence: Rhetoric versus data. *Psychology of Popular Media Culture*, *4*(4), 277–295.
- Mathewson, K. E., Basak, C., Maclin, E. L., Low, K. A., Boot, W. R., Kramer, A. F., . . . Gratton, G. (2012). Different slopes for different folks: Alpha and delta EEG power

- predict subsequent video game learning rate and improvements in cognitive control tasks. *Psychophysiology*, *49*(12), 1558–1570.
- McAdams, C. J., & Maunsell, J. H. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *Journal of Neuroscience*, *19*(1), 431–441.
- Mihara, S., & Higuchi, S. (2017). Cross-sectional and longitudinal epidemiological studies of internet gaming disorder: A systematic review of the literature. *Psychiatry and Clinical Neurosciences*, *71*(7), 425–444.
- Mishra, J., Zinni, M., Bavelier, D., & Hillyard, S. A. (2011). Neural basis of superior performance of action videogame players in an attention-demanding task. *Journal of Neuroscience*, *31*(3), 992–998.
- Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., Howerter, A., & Wager, T. D. (2000). The unity and diversity of executive functions and their contributions to complex “frontal lobe” tasks: A latent variable analysis. *Cognitive Psychology*, *41*(1), 49–100.
- Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, *229*(4715), 782–784.
- Nenert, R., Viswanathan, S., Dubuc, D. M., & Visscher, K. M. (2012). Modulations of ongoing alpha oscillations predict successful short-term visual memory encoding. *Frontiers in Human Neuroscience*, *6*, 127.
- Neubauer, A. C., & Fink, A. (2009). Intelligence and neural efficiency: Measures of brain activation versus measures of functional connectivity in the brain. *Intelligence*, *37*(2), 223–229.
- Noonan, M. P., Adamian, N., Pike, A., Printzlau, F., Crittenden, B. M., & Stokes, M. G. (2016). Distinct mechanisms for distractor suppression and target facilitation. *Journal of Neuroscience*, *36*(6), 1797–1807.
- Pang, J. C., & Robinson, P. A. (2018). Neural mechanisms of the EEG alpha-BOLD anticorrelation. *Neuroimage*, *181*, 461–470.

- Peylo, C., Hilla, Y., & Sauseng, P. (2021). Cause or consequence? Alpha oscillations in visuospatial attention. *Trends in Neurosciences*, *44*(9), 705–713.
- Qin, N., Wiens, S., Rauss, K., & Pourtois, G. (2022). Effects of selective attention on the C1 ERP component: A systematic review and meta-analysis. *Psychophysiology*, *59*(12), e14123.
- Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron*, *26*(3), 703–714.
- Riddle, J., Scimeca, J. M., Cellier, D., Dhanani, S., & D’Esposito, M. (2020). Causal evidence for a role of theta and alpha oscillations in the control of working memory. *Current Biology*, *30*(9), 1748–1754.
- Rihs, T. A., Michel, C. M., & Thut, G. (2009). A bias for posterior α -band power suppression versus enhancement during shifting versus maintenance of spatial attention. *Neuroimage*, *44*(1), 190–199.
- Roesner, M., Arnau, S., Skiba, I., Wascher, E., & Schneider, D. (2020). The spatial orienting of the focus of attention in working memory makes use of inhibition: Evidence by hemispheric asymmetries in posterior alpha oscillations. *Neuropsychologia*, *142*, 107442.
- Rypma, B., Berger, J. S., Genova, H. M., Rebbecki, D., & D’Esposito, M. (2005). Dissociating age-related changes in cognitive strategy and neural efficiency using event-related fMRI. *Cortex*, *41*(4), 582–594.
- Sauseng, P., Feldheim, J. F., Freunberger, R., & Hummel, F. C. (2011). Right prefrontal TMS disrupts interregional anticipatory EEG alpha activity during shifting of visuospatial attention. *Frontiers in Psychology*, *2*, 241.
- Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., . . . Hummel, F. C. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology*, *19*(21), 1846–1852.
- Schenk, S., Lech, R. K., & Suchan, B. (2017). Games people play: How video games improve probabilistic learning. *Behavioural Brain Research*, *335*, 208–214.

- Schlickum, M. K., Hedman, L., Enochsson, L., Kjellin, A., & Felländer-Tsai, L. (2009). Systematic video game training in surgical novices improves performance in virtual reality endoscopic surgical simulators: A prospective randomized study. *World Journal of Surgery*, *33*(11), 2360–2367.
- Schubert, T., Finke, K., Redel, P., Kluckow, S., Müller, H., & Strobach, T. (2015). Video game experience and its influence on visual attention parameters: An investigation using the framework of the theory of visual attention (TVA). *Acta Psychologica*, *157*, 200–214.
- Schurgin, M. W., Wixted, J. T., & Brady, T. F. (2020). Psychophysical scaling reveals a unified theory of visual memory strength. *Nature Human Behaviour*, *4*(11), 1156–1172.
- Smit, C. M., Wright, M. J., Hansell, N. K., Geffen, G. M., & Martin, N. G. (2006). Genetic variation of individual alpha frequency (IAF) and alpha power in a large adolescent twin sample. *International Journal of Psychophysiology*, *61*(2), 235–243.
- Snyder, A. C., & Foxe, J. J. (2010). Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: A high-density electrical mapping study. *Journal of Neuroscience*, *30*(11), 4024–4032.
- Spaak, E., Fonken, Y., Jensen, O., & Lange, F. P. de. (2016). The neural mechanisms of prediction in visual search. *Cerebral Cortex*, *26*(11), 4327–4336.
- Stevens, M. W., Dorstyn, D., Delfabbro, P. H., & King, D. L. (2021). Global prevalence of gaming disorder: A systematic review and meta-analysis. *Australian & New Zealand Journal of Psychiatry*, *55*(6), 553–568.
- Strobach, T., Frensch, P. A., & Schubert, T. (2012). Video game practice optimizes executive control skills in dual-task and task switching situations. *Acta Psychologica*, *140*(1), 13–24.
- Tanaka, S., Ikeda, H., Kasahara, K., Kato, R., Tsubomi, H., Sugawara, S. K., . . . Watanabe, K. (2013). Larger right posterior parietal volume in action video game experts: A behavioral and voxel-based morphometry (VBM) study. *Plos One*, *8*(6), e66998.
- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). α -band

- electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, *26*(37), 9494–9502.
- Töllner, T., Gramann, K., Müller, H. J., & Eimer, M. (2009). The anterior N1 component as an index of modality shifting. *Journal of Cognitive Neuroscience*, *21*(9), 1653–1669.
- Treisman, A., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*(1), 97–136.
- Treisman, A., & Sato, S. (1990). Conjunction search revisited. *Journal of Experimental Psychology: Human Perception and Performance*, *16*(3), 459–478.
- Van Boxtel, J. J., Tsuchiya, N., & Koch, C. (2010). Consciousness and attention: On sufficiency and necessity. *Frontiers in Psychology*, *1*, 217.
- van Diepen, R. M., Miller, L. M., Mazaheri, A., & Geng, J. J. (2016). The role of alpha activity in spatial and feature-based attention. *ENeuro*, *3*(5), 1–11.
- Vialatte, F.-B., Maurice, M., Dauwels, J., & Cichocki, A. (2010). Steady-state visually evoked potentials: Focus on essential paradigms and future perspectives. *Progress in Neurobiology*, *90*(4), 418–438.
- Wildegger, T., van Ede, F., Woolrich, M., Gillebert, C. R., & Nobre, A. C. (2017). Preparatory α -band oscillations reflect spatial gating independently of predictions regarding target identity. *Journal of Neurophysiology*, *117*(3), 1385–1394.
- Wilms, I. L., Petersen, A., & Vangkilde, S. (2013). Intensive video gaming improves encoding speed to visual short-term memory in young male adults. *Acta Psychologica*, *142*(1), 108–118.
- Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific α -band electroencephalography increases over occipital cortex. *Journal of Neuroscience*, *20*(6), RC63–RC63.
- World Health Organisation. (2019/2020). *International classification of diseases, eleventh revision (ICD-11)*. World Health Organisation. Retrieved from <https://icd.who.int/browse11>

- Wu, S., Cheng, C. K., Feng, J., D'angelo, L., Alain, C., & Spence, I. (2012). Playing a first-person shooter video game induces neuroplastic change. *Journal of Cognitive Neuroscience*, *24*(6), 1286–1293.
- Zhao, Y., & Zhu, Y. (2021). Identity transformation, stigma power, and mental wellbeing of chinese eSports professional players. *International Journal of Cultural Studies*, *24*(3), 485–503.
- Zhigalov, A., & Jensen, O. (2020). Alpha oscillations do not implement gain control in early visual cortex but rather gating in parieto-occipital regions. *Human Brain Mapping*, *41*(18), 5176–5186.

Acknowledgments

- **Paul Sauseng:** Paul, thank you for believing in me and supporting me as my mentor. There had been times when I doubted myself. But you always managed to cheer me up and keep me going. Even if that meant I would show up dressed as an axolotl at a conference.
- **Heinrich René Liesefeld, Laura Busse, Anne Frenzel:** René, Laura and Anne, thank you so much for your emotional and professional support as members of my Thesis Advisory Committee.
- **Julia Föcker:** Julia, thank you so much for supporting me in starting this journey. Your work inspired me and represented the foundation of my thesis.
- **Anna Lena Biel, Charline Peylo, Elisabeth Friedrich:** Anna Lena, Charline and Lisa, thank you for being the best colleagues ever. I hope we will keep in touch and I wish you the best of luck for your futures.
- **Fabian Link:** Fabibi, thank you for being the best student assistant someone could wish for and becoming one of my closest friends. I have to admit some of my projects would not have worked out if it had not been for your effort and dedication.
- **Jörg Alejandro von Mankowski:** Alejandro, thank you for always being by my side no matter how stormy the circumstances. Indeed, I could not have achieved this without your patience and support.
- **(Baby) Otters:** Watching (baby) otters may do wonders in lifting the mood.
- **Family and Friends:** Thank you all so much for being part of my life.
- **Graduate School of Systemic Neurosciences:** Thank you for everything.

Curriculum Vitae

Education

Year	Degree	Dissertation	Institution
10/2020 – present	PhD Systemic Neurosciences	NeuroGame: Neural Mechanisms Underlying Cognitive Improvement in Video Gamers	LMU, Munich, Germany
10/2017 – 09/2019	M.Sc. Neuro-Cognitive Psychology	Associations between Brain Oscillations and TVA Parameters in Action Video Gamers	LMU, Munich, Germany
10/2014 – 09/2017	B.Sc. Psychology, Psychopathology & Clinical Neuropsychology	Eine wissenschaftliche Evaluation des Phönix Programms – Ein Interventionsprogramm für Gewaltstraftäter der Landgerichte Munich I und II	LMU, Munich, Germany

Note: LMU: Ludwig-Maximilians-Universität

Professional Experiences

Year	Role	Details	Institution
06/2022 - present	Research Assistant <i>Experimental Psychology</i>	<ul style="list-style-type: none"> <i>Research Focus:</i> Multitasking <i>Teaching:</i> Experimental Research Internship for Under- and Graduate Students	Universität der Bundeswehr, Neubiberg, Germany

10/2019 – 05/2022	Research Assistant <i>Biological Psychology</i>	<ul style="list-style-type: none"> <i>Research Focus:</i> Neuronal Substrates of Video Gaming Effects <i>Methodology:</i> Electroencephalography (EEG), transcranial Alternating Current Stimulation (tACS), Computational Modeling e.g., based on Theory of Visual Attention (TVA) <i>Teaching:</i> Undergraduate Research Projects 	LMU, Munich, Germany
10/2018 – 09/2019	Graduate Research Assistant <i>Biological Psychology</i>	<ul style="list-style-type: none"> <i>Research Focus:</i> Neural Substrates of (a)typical Visual/Verbal/Social Working Memory <i>Methodology:</i> EEG 	LMU, Munich, Germany
04/2017 – 09/2018	Student/ Graduate Research Assistant <i>Psychological Methods and Diagnostics</i>	<ul style="list-style-type: none"> <i>Tutoring:</i> 20-30 undergraduate students, 90 min per week <i>Topics:</i> Descriptive/Inferential Statistics 	LMU, Munich, Germany

Scholarships

Year	Title	Details	Institution
06/2022 - 12/2022	LMU-Abschlusstipendium	Financial Support until the submission of the dissertation. In total, 6618 Euro.	GraduateCenter, Munich, Germany

List of Publications

Journal Contributions

- **Hilla, Y.**, Link, F., & Sauseng, P. (2022). Alpha-tACS alters attentional control but not cognitive functions as video games do: A psychophysical investigation based on the theory of visual attention. *European Journal of Neuroscience*, *57*(10), 1705–1722.
- Peylo, C., **Hilla, Y.**, & Sauseng, P. (2021). Cause or consequence? Alpha oscillations in visuospatial attention. *Trends in Neurosciences*, *44*(9), 705-713. (Shared first-authorship)
- **Hilla, Y.**, Von Mankowski, J., Föcker, J., & Sauseng, P. (2020). Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation. *Frontiers in Psychology*, *11*, 599788.

Conference Contributions

- Stefani, M., **Hilla, Y.**, & Mack, Wolfgang (2023, March). *Multitasking-Tasks Predict Naturalistic Multitasking Better than Multitasking Costs: Evidence from a Laboratory-Field Study*. Talk presented at 65th TeaP - Tagung experimentell arbeitender Psychologen (Conference of Experimental Psychology), Trier, Germany.
- **Hilla, Y.**, Link, F., & Sauseng, P. (2022, July). *Not in Control After All - Reasons Why Attentional Control Unlikely Predicts Differential Cognitive Processing in Video Gamers*. Poster presented at Salzburg Mind Brain Annual Meeting 2022 (SAMBA 2022), Salzburg, Austria.
- **Hilla, Y.**, Link, F., & Sauseng, P. (2022, June). *Does Transcranial Alternating Current Stimulation at Alpha Frequency Induce Similar Alterations in Theory of Visual Attention Cognitive Functions as Video Games?*. Poster presented at 47. Tagung Psychologie und Gehirn, Freiburg, Germany.
- **Hilla, Y.**, Link, F., & Sauseng, P. (2022, May). *Differences in Theory of Visual Attention Cognitive Functions Between Video and Non-Video Gamers are Associated*

with Differential Alpha Amplitude Modulations. Poster presented at International Conference of Cognitive Neuroscience 2022 (ICON 2022), Espoo, Finland.

- **Hilla**, Y., & Sauseng, P. (2021, June). *The Role of EEG Alpha Oscillations in TVA Parameter Values*. Poster presented at 46. Jahrestagung Psychologie und Gehirn, Tübingen, Germany.
- **Hilla**, Y., von Mankowski, J., Föcker, J., & Sauseng, P. (2021, March). *Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation*. Talk presented at 63rd TeaP - Tagung experimentell arbeitender Psychologen (Conference of Experimental Psychology), Ulm, Germany.

Eidesstattliche Versicherung/Affidavit

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation *NeuroGame: Neural Mechanisms Underlying Cognitive Improvement in Video Gamers* selbstständig angefertigt habe, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

I hereby confirm that the dissertation *NeuroGame: Neural Mechanisms Underlying Cognitive Improvement in Video Gamers* is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

München/Munich

Yannik Hilla

17th January 2023

Datum/Date

Unterschrift/Signature

Declaration of Author Contributions

Cause or Consequence? Alpha Oscillations in Visuospatial Attention

- Peylo, C., **Hilla**, Y., & Sauseng, P. (2021). Cause or consequence? Alpha oscillations in visuospatial attention. *Trends in Neurosciences*, 44(9), 705-713.
- C.P.: Conceptualization, Writing - Review & Editing. **Y.H.**: Conceptualization, Writing - Review & Editing. P.S.: Conceptualization, Writing - Review & Editing, Funding Acquisition, Resources, Validation.
- Charline Peylo and I contributed equally to conceptualizing, writing, reviewing and editing the article (shared first-authorship).

_____ _____ _____
Charline Peylo Yannik Hilla Paul Sauseng

Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation

- **Hilla, Y.**, Von Mankowski, J., Föcker, J., & Sauseng, P. (2020). Faster Visual Information Processing in Video Gamers Is Associated With EEG Alpha Amplitude Modulation. *Frontiers in Psychology, 11*, 599788.
- **Y.H.:** Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Project Administration, Software Development, Writing - Review & Editing. **J.M.:** Software Development, Writing - Review & Editing. **J.F.:** Conceptualization, Validation, Writing - Review & Editing. **P.S.:** Conceptualization, Funding Acquisition, Resources, Validation, Writing - Review & Editing.
- I developed the experimental design of this study. This included a comprehensive literature research and developing software to run the task. Moreover, I personally conducted the research. Furthermore, I analyzed the data and performed statistical tests. Furthermore, I wrote the the manuscript to summarize the results of our research, and reviewed and edited the manuscript. Also, I took care of data curation, e.g., anonymization, etc.

Yannik Hilla Paul Sauseng

Alpha-tACS Alters Attentional Control but not Cognitive Functions as Video Games Do

- **Hilla, Y., Link, F., & Sauseng, P (2022).** Alpha-tACS alters attentional control but not cognitive functions as video games do: A psychophysical investigation based on the theory of visual attention. *European Journal of Neuroscience*, 57(10), 1705–1722.
- **Y.H.:** Conceptualization, Methodology, Project Administration, Investigation, Data Curation, Formal Analysis, Visualization, Software, Writing - Original Draft Preparation, Writing - Review & Editing. **F.L.:** Investigation, Data Curation. **P.S.:** Conceptualization, Funding Acquisition, Methodology, Resources, Supervision, Validation, Writing - Review & Editing.
- I developed the experimental design of this study. This included a comprehensive literature research and developing software to run the task. Moreover, I personally conducted the research. Furthermore, I analyzed the data and performed statistical tests. Furthermore, I wrote the manuscript to summarize the results of our research, and reviewed and edited the manuscript. Also, I took care of data curation, e.g., anonymization, etc.

Yannik Hilla Paul Sauseng