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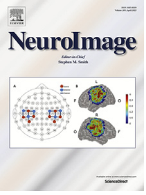

Enhanced temporal resolution of vision in action video game players[☆],[☆☆]

Francois R Foerster[a,*], Matthieu Chidharom[b], Anne Giersch[a]

[a] *Université de Strasbourg, INSERM U1114, Pôle de Psychiatrie, Centre Hospitalier Régional Universitaire de Strasbourg, France*
[b] *Department of Psychology, Lehigh University, Bethlehem, PA, United States*

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ABSTRACT

Video game play has been suggested to improve visual and attention processing. Nevertheless, while action video game play is highly dynamic, there is scarce research on how information is temporally discriminated at the millisecond level. This cross-sectional study investigates whether temporal discrimination at the millisecond level in vision varies across action video game players (VGPs; $N = 23$) and non-video game players (NVGPs; $N = 23$). Participants discriminated synchronous from asynchronous onsets of two visual targets in virtual reality, while their EEG and oculomotor movements were recorded. Results show an increased sensitivity to short asynchronies (11, 33 and 66 ms) in VGPs compared with NVGPs, which was especially marked at the start of the task, suggesting better temporal discrimination abilities. Pre-targets oculomotor freezing – the inhibition of small fixational saccades – was associated with correct temporal discrimination, probably revealing attentional preparation. However, this parameter did not differ between groups. EEG and reconstruction analyses suggest that the enhancement of temporal discrimination in VGPs during temporal discrimination is related to parieto-occipital processing, and a reduction of alpha-band (8–14 Hz) power and inter-trial phase coherence. Overall, the study reveals an enhanced ability in action video game players to discriminate in time visual events in close temporal proximity combined with reduced alpha-band oscillatory activities. Consequently, playing action video games is associated with an improved temporal resolution of vision.

1. Introduction

Temporal discrimination is the ability to consciously discriminate in time one sensory event from another and is the foundation of adaptive behaviors (Mauk and Buonomano, 2004). Distinguishing successive events from one another is indeed necessary to follow and adapt to the flow of successive information. Temporal discrimination skills at the millisecond level have been studied through simultaneity judgment (SJ) tasks (also called asynchrony detection tasks), which evaluate one's ability to detect the temporal gap separating the onset of two sensory events. This detection of asynchronies has been found altered in people with autism spectrum disorders (Falter et al., 2012), developmental dyslexia (for a review, see Meilleur et al., 2020) and schizophrenia, in many modalities and especially in vision (Di Cosmo et al., 2021; Foucher et al., 2007; Giersch et al., 2009; Lalanne et al., 2012; Marques-Carneiro et al., 2021; Martin et al., 2013; Schmidt et al., 2011; Stevenson et al., 2017). Clinical symptoms are related to these temporal alterations (Foucher et al., 2007; Giersch et al., 2015; Martin et al., 2017, 2014). Unfortunately, these symptoms persist with medication, as hitherto dopamine does not appear involved (Chassignolle et al., 2021). Nonetheless, new leads for treatment may be found in video game studies.

Our ability to detect visual asynchronies can be improved through computer-based tasks (Virsu et al., 2008). Video games might induce a similar benefit. Indeed, visual (Bejjanki et al., 2014; Buckley et al., 2010; Green and Bavelier, 2007; Pohl et al., 2014; West et al., 2008)

Abbreviations: VGP, Video Game Player; NVGP, Non-Video Game Player; SOA, Stimulus Onset Asynchrony; ITC, Inter-trial Phase Coherence; VR, Virtual Reality.

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[☆☆] Significance Statement In fast-paced action video games, players constantly face challenging situations where prevailing depends on the rapid detection of visual signals to guide behaviors. Previous research showed enhancement of temporal discrimination of audiovisual signals in action video game players compared with non-gamers. Yet, whether the locus of this enhancement is limited to multimodal processing or extended to a more fundamental (unisensory) level was unclear so far. Here, we provide behavioral and neuronal evidence of an enhanced ability to consciously detect a delay as short as 11 ms between two visual signals in action video game players. This suggests that intense fast-paced visuo-motor practices through video game play are associated with a higher temporal resolution of visual processing.

[*] Corresponding author.
E-mail address: francoisfoerster@gmail.com (F.R. Foerster).

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and temporal (Donohue et al., 2010; Rivero et al., 2012) abilities at the millisecond level have been found enhanced in action video game players. While several studies showed improved visual processing associated with video game play, sometimes for short duration stimuli (Föcker et al., 2019; Green and Bavelier, 2003; Krishnan et al., 2013; Li et al., 2010; Mishra et al., 2011; Pohl et al., 2014; Schubert et al., 2015; Wilms et al., 2013), they are based on tasks involving attention, discrimination of stimuli displayed simultaneously, or in the same location. Temporal discrimination skills, i.e. the ability to detect that two distinct signals are not displayed simultaneously, was not directly evaluated in these studies. Only Donohue et al. (2010) reported an enhanced asynchrony detection between visual and auditory stimuli in action video game players (VGPs) compared with non-video game players (NVGPs). Crucially, whether this enhanced skill is specific to multisensory conditions is unclear. For example, this enhancement may relate to asymmetric processing of visual and auditory information, or the need to compare the moment of sensory occurrence across two different modalities. If the enhancement of temporal discrimination abilities in VGPs generalizes to unisensory visual conditions, it would suggest an enhancement of the temporal aspect of sensory discrimination rather than multisensory processing. It could then represent the basis for a new regime of cognitive remediation for pathologies like schizophrenia.

The goal of this study is to test the hypothesis of enhanced millisecond-level temporal discrimination skills in VGPs in the visual modality. Knowing which aspects of temporal discrimination (preparation or asynchrony processing) are improved in video game players is required to target specific mechanisms during remediation. To that aim, we use EEG and eye-tracking recordings to distinguish the preparation phase from the asynchrony processing. Although there is scarce data on EEG and asynchrony processing, we ground our analysis on what is known about perceptual processing.

In psychophysical tasks such as the SJ task, perceptual discrimination is tightly related to both preparatory and target processing. On the one hand, parieto-occipital alpha-band (8–14 Hz) oscillations contribute to the preparation of visual processing (Mathewson et al., 2009; Thut et al., 2006) and are associated with temporal attention (Hanslmayr et al., 2011). For instance, the decrease of prestimulus alpha power facilitates the detection of a forthcoming target (Babiloni et al., 2006; Ergenoglu et al., 2004; Harris et al., 2020; Jensen and Mazaheri, 2010; Klimesch, 1999; Lange et al., 2013; Zhou et al., 2021) by modulating cortical excitability (Iemi et al., 2017; Jensen et al., 2014; Jensen and Mazaheri, 2010; Klimesch et al., 2011, 2007) or through gating mechanisms (Gundlach et al., 2020; Zhigalov and Jensen, 2020). In a SJ task, temporal discrimination of tactile stimuli at the millisecond-level depends on prestimulus alpha power (Baumgarten et al., 2016). Hence, prestimulus alpha power reflects different states of preparedness to sensory and attention processing. Similarly, small eye movements occurring before stimulation reveal different states of preparedness and are associated with perceptual discrimination. The inhibition of small fixational saccades (also called oculomotor freezing; Abeles et al., 2020; Amit et al., 2019; Badde et al., 2020; Tal-Perry and Yuval-Greenberg, 2020) reflects stimulus anticipation and helps visual discrimination (Denison et al., 2019). On the other hand, perceptual discrimination also depends on mechanisms operating during the processing of the target itself. A stimulus onset can induce a functional disinhibition of neurons in task-relevant cortical regions, reflected in the decrease of alpha-band power (Jensen and Mazaheri, 2010; Klimesch et al., 2011). For instance, detecting a target presented at the perceptual threshold is accompanied by posterior alpha-band power decreases (Babiloni et al., 2006), supporting the idea that a decrease in alpha-band power reflects to some extent visual awareness (Harris et al., 2020). Also, post-stimulus alpha-band power decrease has been associated with improved speed of visual information processing within the 'theory of visual attention' framework (Hilla et al., 2020). Overall, this means that temporal discrimination abilities in vision can be reflected in both pre- and post-target posterior alpha-band power decreases. In this cross-sectional study, EEG and eye-tracking data are used to evaluate whether preparatory processing, target processing, or both could explain the potential enhancement of temporal discrimination skills in VGPs.

To evaluate temporal discrimination skills in VGPs and NVGPs, participants performed a SJ task and were instructed to discriminate synchronous from asynchronous onsets of two targets. The targets, presented in the left and right visual fields, were either presented simultaneously (0 ms stimulus onset asynchrony; SOA) or asynchronously (11, 33 or 66 ms SOA). Here, if temporal discrimination skills are improved in VGP compared with NVGPs, then the results already observed with audiovisual modalities (Donohue et al., 2010) should generalize to the unisensory visual modality. In signal detection theory terms (Stanislaw and Todorov, 1999), VGPs should exhibit higher perceptual sensitivities (*d'* values) than NVGPs. The learning-to-learn account (Bejjanki et al., 2014; Green et al., 2010; Zhang et al., 2021) suggests that VGPs outperform NVGPs due to an increased ability to learn the key properties of a task. When facing novel tasks, inferring the probabilities of task parameters must be learned through practice. Such a probabilistic inference enhancement could, in turn, improve attentional control in switching attention modes at the most appropriate moments. According to the learning-to-learn account, increased perceptual sensitivities in VGPs either at the beginning or at the end of the task would contrast with or support the hypothesis, respectively. To investigate the neurocognitive basis of temporal discrimination skills in VGPs and NVGPs, we created an original setup combining immersive virtual reality, head-mounted eye-tracking system and EEG recordings. Not only virtual reality helps to get closer to ecological conditions (e.g. 3D perception and immersion) than desktop settings, it also facilitates the commitment to the task and allows to track eye movements using the embedded eye-tracking system of the headset.

2. Method

2.1. Participants

Recent discussions highlighted that recruitment strategies can influence video gaming effects on perception and cognition (Boot et al., 2011; Denkinger et al., 2021). For example, if gamers know they are recruited because of their gaming habit, it may motivate them to perform well. In this cross-sectional study, participants were chosen using overt recruitment and screening criteria and were informed that the study explores the limits of time perception. They were not informed about the different asynchronies. The screening criteria to categorize VGPs and NVGPs was assessed through a questionnaire asking which games they had been playing over the last 12 months, over what period of time in months, and the average time spent playing each game per week. In accordance with previous studies (Bavelier et al., 2012; Bejjanki et al., 2014; Föcker et al., 2018), the criterion to be considered a VGP was a minimum of 5 h per week of action video game practice for the previous 12 months. The games included mainly first-person shooters (e.g. Call of Duty series, Apex Legends, Overwatch, Counter Striker series), real-time strategy (Starcraft II) and multiplayer online battle arenas (e.g. Leagues of Legends, Heroes of the Storm) which mix the characteristics of action and real-time strategy games. All these games have been proposed to involve the same types of cognitive functions (see e.g. Large et al., 2019), and require high-paced visual processing. The latter is especially pertinent relative to time processing and our study. The VGP group included 23 participants (4 females, 2 left-handed, age $M = 25.2$; SD = 5.7). The play time of VGPs ranged from 12 to 34 h a week over the last 12 months before testing. The criterion to be included in the NVGP group was little or no action video game practice for a minimum of one year, although no extensive practice ever ($N = 16$) was highly favored. The NVGP group was composed of 23 participants (7 females, 5 left-handed, age $M = 26.8$; SD = 4.6). The play time of NVGPs ranged from 0 to 5 h a week over the last 12 months before testing. T- and

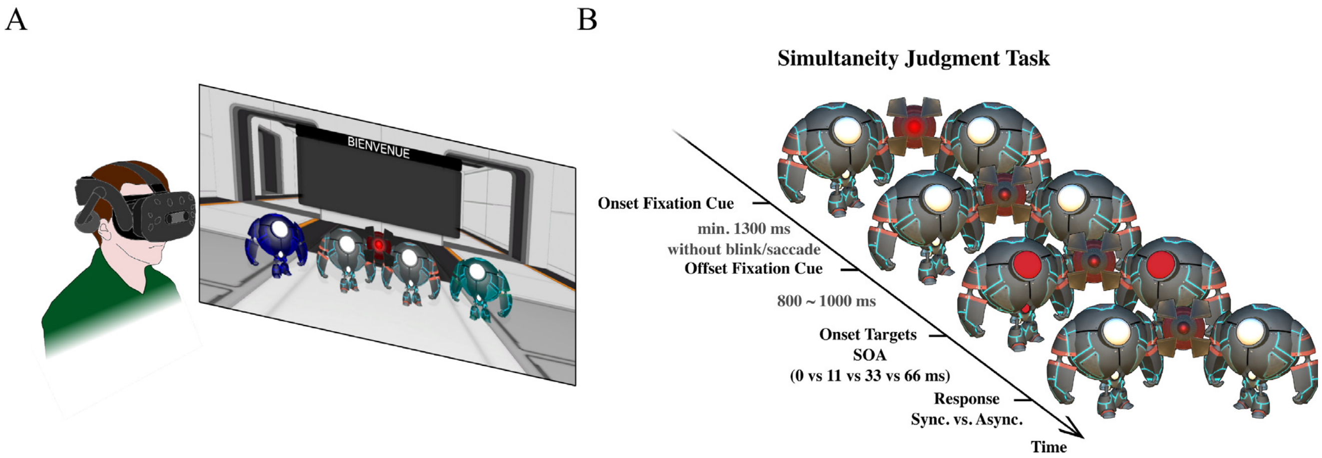

Fig. 1. Setup and experimental task. Action video game players (VGPs, $N = 23$) and non-video game players (NVGPs, $N = 23$) were exposed to robots in virtual reality and performed a simultaneity judgment task (A). Using buttons of the controller, the task of the participants was to judge whether the onset of two visual targets (red lights; B) was simultaneous (0 ms SOA) or asynchronous (11 ms, 33 ms or 66 ms SOA). Reaction times, eye-tracking, and EEG measures were used to evaluate how VGPs and NVGPs anticipated and processed these visual asynchronies.

Chi^2-tests revealed no difference in age ($p = .312$) or gender ($p = .391$) between VGPs and NVGPs. However, the education level was lower in NVGPs (mean = 14.3 years) than VGPs (mean = 15.7 years, $p = .012$). Twelve years of education represent the end of high school and 15 years represent a bachelor degree. All subjects had normal or corrected-to-normal visual acuity, as verified with the Freiburg Visual Acuity Test (Bach, 1996). No participants reported color-blindness. The exposure to VR experience was not quantified in this experiment. However, no participant reported any feeling of cybersickness during or after the experiment. It should be noted that our sample of participants has been involved in another related study (Foerster et al., 2022). The sample size of participants was equal or larger than recent cross-sectional gaming studies (e.g. Cui et al., 2021; Gong et al., 2019; Pöhlmann et al., 2022). An overall post-hoc statistical power of 59% was estimated for a mixed ANOVA with the current experimental design, with an $\alpha = 0.05$ and a sample size $n = 23$ per group ($N_{VGP} = 23$; $N_{NVGP} = 23$). All participants provided written informed consent to take part in the study and were given a compensation of 45€ for their participation. The study has been approved by the local ethics committee (i.e. Comité d'Éthique de Recherche) of the University of Strasbourg.

2.2. *Virtual reality setup*

The experiment used the Unity software (Unity technologies, v. 2019.3.9f1) to create the virtual environment. The HTC Vive Eye Pro (HTC Corp.) controllers and headset were used to immerse the participants in VR. Participants wore both the VR and EEG headsets while sitting on a chair. The VR headset was adjusted to each participant, which allowed us to avoid physical strain on the EEG electrodes. The headset is comfortable and does not induce sweating. Several benefits motivated the use of VR to perform the task. Firstly, making the task more entertaining facilitates the engagement of the participant. Secondly, VR allows a better trade-off between fully-controlled experimental settings and conditions close to everyday life. Three-dimensional visual percepts are indeed considered as more realistic in comparison with 2D screen setups (Snow and Culham, 2021). Thirdly, the embedded eye-tracking system in the VR headset allows to track and record the gaze in the 3D space. The eye-tracking system was used to trigger the visual stimuli contingently with the gaze location and following a time interval free of saccades and eye-blinks. Each participant was immersed in a virtual room and was facing four 3D animated robots. The experiment was composed of two intertwined tasks: a SJ task and a variable foreperiod task (Foerster et al., 2022). Details about the variable foreperiod task can be found in the Supplemental Materials.

2.3. *Simultaneity judgment task and stimuli*

At the beginning of each trial, a red light representing a fixation cue appeared in between the two central robots displayed in the center of the visual field (Fig. 1). The robots were always in the same localization and their spatial localization was easy to discriminate. The fixation cue disappeared following 1300 ms of gaze fixation without blinking or saccades away from the cue. In case of a blink, the fixation cue remained until the participant reached 1300 ms free of blink and saccades. All participants managed to fixate the cue without blinking. After a random inter-stimulus interval (ranging from 800 to 1000 ms), visual targets appeared and remained on the screen until the participant's response. These targets consisted of two red lights, each in one of the two centrally located robots. These targets occurred either simultaneously (i.e. 0 ms SOA) or asynchronously with a SOA of 11 ms, 33 ms or 66 ms. The order of the targets (right-left or left-right) was randomized across trials. Following the appearance of the targets, the task of the participant was to judge whether the targets appeared simultaneously or asynchronously. Participants gave their response by pressing the trigger button or the pad button of the controller placed in their right hand. No response time limit was implemented. The next trial started 1000 ms after the participant's response. The matching of the controller buttons with the simultaneous/asynchronous judgments was randomly assigned for each participant. The procedure consisted of four blocks of 120 trials. Each block included 30 trials of each SOA displayed in randomized order. The targets were presented at a distance of four meters from the participant, and located at 8° of visual angle from the participant's facing direction. Participants were instructed that SOAs could be long, very short or null. The different SOAs were presented in a within-block design and displayed in random order.

2.4. *Behavioral parameters*

We applied signal detection theory (Stanislaw and Todorov, 1999) to discriminate between two aspects of the participants' response: the perceptual sensitivity (*d'*) representing the ability to discriminate between asynchrony and simultaneity, and the decisional bias (criterion *c*) representing the tendency to report seeing an asynchrony independently of the SOA.

2.5. *Eye-tracking*

Binocular gaze position was monitored using the eye-tracking system (Tobii Ltd.) embedded in the VR headset with a sampling rate of

90 Hz and an estimated spatial accuracy between 0.5° to 1.1° The particularity of such a system is that (1) it tracks eye movements corrected for head movements, (2) it provides estimations of the gaze location in the 3D space rather than on-screen 2D space, 3) the calibration-free data recording for saccades analysis renders the measure non-intrusive. Here we analyzed the likelihood of small fixational saccades prior targets' appearance, as previously investigated (Denison et al., 2019). Saccades of all sizes were included, but due to the task requirements to fixate the target area, most saccades were small (1.4° of visual angle on average).

At first, the onsets of blinks were identified with the HTC SRanipal SDK, detecting blinks via individual eye openness. Because blinks were rare events given the non-blinking requirements to trigger the fixation cue offset, trials containing at least one blink occurring around the onset of the targets (i.e. –600 ms to 200 ms) were discarded (4.8% of total trials). Then, raw data of each trial were interpolated with a spline method to increase the temporal precision, followed by the calculations of the derivations of the speed of the vertical and horizontal eye movements.

Saccades were detected using an established algorithm (Engbert, 2006) based on the gaze's velocities. An elliptic threshold criterion for saccades detection was determined in 2D velocity space based on the horizontal and the vertical velocities of the eye movement. As in previous studies (Denison et al., 2019; Rolfs et al., 2008), we set the threshold to be six times the SD of the eye-movement velocity, using a median-based estimate of the SD. This SD estimate was set based on the velocities calculated for each trial. Saccade onsets were defined when six or more consecutive velocity samples (i.e. a minimum of 6 ms) were outside the ellipse.

We controlled for corrective saccades following overshoot, which could have been confused with saccades. To do so, saccades were discarded when separated by less than 50 ms from the preceding one. We verified that the velocity and the magnitude of the saccades were correlated as usual ($r = 0.71$, $p < 10^{-6}$), thus confirming a low false alarm rate of the saccade detection algorithm (Zuber et al., 1965).

Saccade rates were smoothed using a moving average window of 100 ms, as in Betta and Turatto (2006). Preliminary analyses compared the results with a moving window of 50 ms (as in Dankner et al., 2017; Denison et al., 2019; Tal-Perry and Yuval-Greenberg, 2020) which did not affect the data interpretation, other than reducing the signal/noise ratio.

2.6. EEG acquisition and processing

EEG activity was continuously collected using a Biosemi ActiveTwo 10–20 system with 64 active channels at 1024 Hz sampling rates and the ActiView software. The electrode offset was kept below 20 mV. The offset values were the voltage difference between each electrode and the CMS-DRL reference channels located to the left and right sides of POz. Electrode impedances were kept below 20 kΩ. EEG analyses were performed with MNE-Python v.0.22.0 (Gramfort et al., 2014, 2013). Raw data were filtered offline with a 0.1 Hz high pass filter and a 40 Hz low pass filter. The Autoreject algorithm (Jas et al., 2017) was used to detect and repair artifacts. The motivation to use this algorithm was to maximize the signal-noise ratio by adapting automatically the artifact detection parameters for each participant. It implements topographic interpolations (Perrin et al., 1989) to correct bad segments. The procedure rejected a mean average of 54 trials (SD = 70) over a total of 480 trials. A surface Laplacian filter was applied (stiffness $m = 4$, $\lambda = 10^{-5}$), resulting in a reference-free current source density (CSD) which increases the spatial resolution of the signal and reduces the signal deformation due to volume conduction (Kayser and Tenke, 2015a, 2015b; Tenke and Kayser, 2012).

2.7. Time-frequency analysis

At first, the continuous EEG signal was segmented into trials locked to the first target onset using a time window starting 1600 ms before the onset and finishing 800 ms after the onset. To analyze the oscillatory activity, time-frequency representations (TFRs) were computed using a wavelet approach (Tallon-Baudry and Bertrand, 1999). A family of Morlet wavelets was built to perform a convolution via a fast Fourier transform over each electrode and each trial. The wavelets were parametrized to extract frequencies from 4 Hz to 40 Hz with a step of 2 Hz. The number of cycles of the wavelets was linearly-spaced, from 3 cycles for the lowest frequency to 10 cycles for the highest frequency. Then, to investigate whether amplitude and phase differed between groups and SOAs before and during the asynchrony processing, we extracted from the TFRs both the signal power and the phase values to compute the inter-trial phase coherence (ITC) values.

The analysis of phase coherence was exploratory and can be found in supplementary materials. Concerning the power analysis, power values were compared to the baseline for each trial. The baseline represented the time-interval starting and finishing 1500 ms and 1000 ms before the first target onset, respectively. Hence, the baseline was a time interval occurring before the offset of the fixation cue. We chose this period for the baseline based on the literature favoring a pre-stimulus baseline period (Gundlach et al., 2020), and to avoid response-related oscillatory signals. Power values were transformed into z-scores using this baseline. We preferred this normalization approach over the baseline-free approach (e.g. Iemi et al., 2017) of power analysis as it increases the signal/noise ratio without eliminating a possible group difference of EEG power before the first target onset. Also, the normalization approach renders the data normally distributed, which allows the use of standard parametric tests. Control analyses of the pre- and post-target onsets alpha power using the baseline-free approach did not change the effects reported below.

Since there is scarce EEG data related with asynchrony detection, we first examined ITC and power values recorded after the first target onset. This qualitative examination revealed two clusters of interest, an alpha-band (8–14 Hz) cluster recorded over parieto-occipital areas and a theta-band (4–8 Hz) cluster recorded over fronto-medial areas. Thus, for statistical analysis, we selected the alpha-band ITC and power recorded at the parieto-occipital electrode POz. The selection of a midline electrode may appear surprising. However, the detection of asynchrony requires a comparison of both stimuli onsets. Moreover, alpha power entails cycles of 100 ms, which unlikely reflect the sequential processing of stimuli at the level of a few tens of milliseconds.

To verify the specificity of our alpha-band effects, we performed a control analysis of the theta-band ITC recorded at the fronto-medial electrode FCz. This control analysis is important also to verify the involvement of oscillatory activity potentially related to attention and cognitive control (Cavanagh and Frank, 2014; Cohen, 2014). Both sites were selected based on previous perceptual studies (Gundlach et al., 2020; Iemi et al., 2019; Zhigalov and Jensen, 2020) and the location of the maximum ITC and power values observed within the two clusters. The number of trials across conditions was equalized to ensure unbiased estimates of ITC and power values. Before statistical analysis, all EEG data were downsampled to 512 Hz to facilitate computations.

2.8. Source reconstruction

We performed a post-hoc source reconstruction to localize the effect of the group on the alpha-band power within the 100–300 ms time window representing the processing period. To do so, individual epochs (non-CSD transformed) were used and filtered in the alpha-band (8–14 Hz) frequencies. Individual forward solutions were created using a 3-layers boundary element model (Hämäläinen and Sarvas, 1989) derived from the MRI template provided in MNE-python. Individual noise covariance matrices were estimated from the baseline time interval (–1500 ms to –1000 ms pre-stimulus period). Then, inverse solutions were applied using the minimum norm method (Hämäläinen and Ilmoniemi, 1994) to estimate the absolute source activation of each participant.

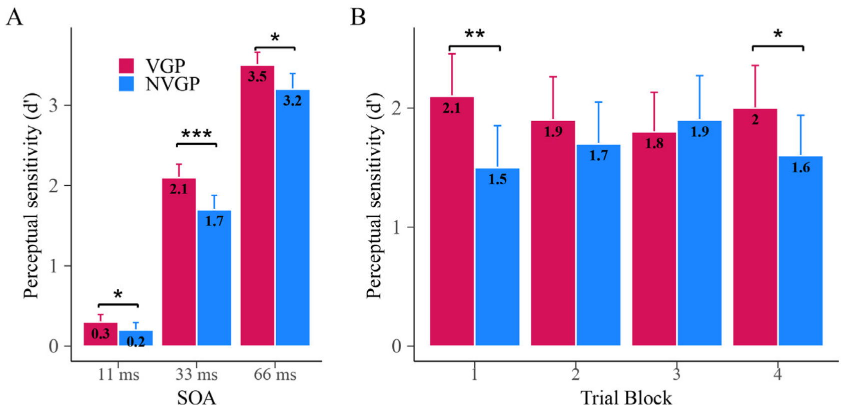

Fig. 2. Behavioral responses to very short visual asynchronies. The analysis of perceptual sensitivity data suggests that VGPs exhibit better detection of very short visual asynchronies (11 ms, 33 ms and 66 ms) than NVGPs (A), especially during the first and last trial blocks (B). Error bars represent one confidence interval of the mean. * $p < .05$, ** $p < .01$, *** $p < .001$.

2.9. Statistical analyses

Time series analyses compared two intervals of interest: (1) the anticipatory period representing the pre-target interval starting from −800 ms and finishing −100 ms before the first target onset, and (2) the processing period representing the interval starting 100 ms and finishing 300 ms after the first target onset. We did not consider the first 100 ms after the first stimulus, since the second stimulus was displayed within this interval, making the interpretation of the results difficult. We also restricted the interval to 300 ms post-stimulus to avoid including response-related signals.

The overall statistical analysis focused on the independent variables Group (VGP vs NVGP), SOA (0, 11, 33 vs 66 ms), Block (trial block 1, 2, 3 vs 4), Time-Window (Preparatory vs Processing period) and Response (Hit vs. Miss, excluding the trials with the 0 ms SOA) and the dependent variables *d', c*, reaction times, percentage of ‘asynchronous’ responses, saccade rates, alpha ITC, alpha power, theta power and lateralization index. The SJ task requires a discrimination between synchronous vs. asynchronous stimuli, which is reflected in the d’. To match the literature (Foucher et al., 2007; Giersch et al., 2009; Lalanne et al., 2012; Marques-Carneiro et al., 2021; Martin et al., 2013; Schmidt et al., 2011; Stevenson et al., 2017) we additionally analyzed the percentage of ‘asynchronous’ responses. The Block effect evaluated whether the pattern of task performance improves or deteriorates over time (cf. the learning-to-learn account). The Response (hit vs. miss) was used only in the analysis of the saccade rates data (else it was the d’ and c criterion). Because some participants never judged 66 ms asynchronies as simultaneous (i.e. a Miss), we compared the saccade rates as a function of misses and hits only in trials with 11 and 33 ms SOA, whereas the analysis of the saccade rates as a function of the SOA included all SOAs. SOA and Response datasets involved an average of 97 trials per condition (min = 90 trials, max = 473 trials) and 102 trials (min = 71 trials, max = 361 trials), respectively.

Repeated-measures mixed analyses of variances (ANOVAs) were performed using R (v. 4.2.1), the dplyr (v. 1.0.5) package, and the rstatix (v. 0.6.0) package with a Greenhouse-Geisser correction when within-subject factors (Block, Response, Time-Window, and SOA) violated the sphericity assumption. Planned comparisons analysis was performed with Tukey’s HSD tests corrected for multiple comparisons with the false-discovery rate method. Shapiro’s test was used to evaluate whether data deviated significantly or not from normal distributions. Pearson’s or Spearman’s correlation analyses were used for normally vs. not normally distributed data respectively (*d’* values and saccade rates, alpha-band ITC and power). Figures were built with the GGplot2 (v. 3.3.0) and gridExtra (v. 2.3) packages in R. The post-hoc statistical power analysis reported above was performed with the package Superpower (v. 0.2.0) in R.

Post-hoc analysis of the source estimates was performed using the non-parametric spatiotemporal cluster-based permutation tests (Maris and Oostenveld, 2007) with the MNE-python function spatio_temporal_cluster_test(). Individual source estimates within the 100–300 ms time window with *t* statistic above the significance threshold of $p < .01$ were clustered. The permutation distribution was approximated from 5000 random permutations of the observed data. Then, for each cluster, we randomly permuted the assignation of individual’s data to either group (VGPs or NVGPs) to test the null hypothesis (i.e. full exchangeability). Only clusters with $p < .01$ are reported.

3. Results

3.1. Task performance

To test the hypothesis that VGPs have a better ability to detect very short asynchronies and whether this ability fluctuated over the course of the experiment, a three-way mixed ANOVA was applied to perceptual sensitivity (*d’*) values with the factors Group, SOA and Block. The analysis revealed a main effect of the Group ($F(1,44) = 4.42$, $p = .045$; $\eta^2_{\text{partial}} = 0.089$) and a main effect of the SOA ($F(2,88) = 524.1$, $p < .0001$; $\eta^2_{\text{partial}} = 0.923$). Additional two-sided paired t-tests confirmed that *d’* values were higher in VGPs relative to NVGPs for all SOAs (11 ms, $p = .0245$, 33 ms, $p = .0008$, 66 ms, $p = .0046$; Fig. 2A). An interaction effect between the Group and the Block was revealed ($F(3,132) = 5.18$, $p = .003$; $\eta^2_{\text{partial}} = 0.105$). Planned comparisons on performance averaged over SOAs showed an increased sensitivity to asynchronies in VGPs relative to NVGPs during the first ($p = .0011$) and last trial blocks ($p = .0297$, see Fig. 2B). The sensitivity fluctuated across blocks in both groups, without clear overall improvement or deterioration. In line with these behavioral results, the analysis of the percentage of ‘asynchrony’ responses also showed that VGPs judged stimuli with 0 ms SOA more often as ‘simultaneous’ compared to NVGPs (see details in Supplemental Materials). This result accounts for the fact that VGPs were better at discriminating synchronous from asynchronous stimuli. No effect of the Group was found on reaction times (see details in Supplemental Materials and Fig. S1). Also, the analysis of the decisional bias (criterion *c*) revealed an interaction effect between the Group, the SOA and the Trial Block: the bias differed between the VGPs and NVGPs only during the third trial block with the SOA of 33 ms (see details in Supplemental Materials; it is interesting to note that this effect occurs in a block in which there is no group effect on *d’*). Overall, these behavioral results indicate that VGPs have better abilities to report milliseconds differences in the onset of two visual stimuli, without extending their response times or using different decision strategies.

3.2. Small fixational saccades prevent short asynchrony detection

Eye-tracking data revealed an oculomotor freezing by showing the gradual decrease, i.e. inhibition of small fixational saccades – reflecting the anticipation of the stimuli (Amit et al., 2019; Betta and Turatto, 2006; Denison et al., 2019). To evaluate whether this saccadic inhibition could explain the increased perceptual sensitivity in VGPs,

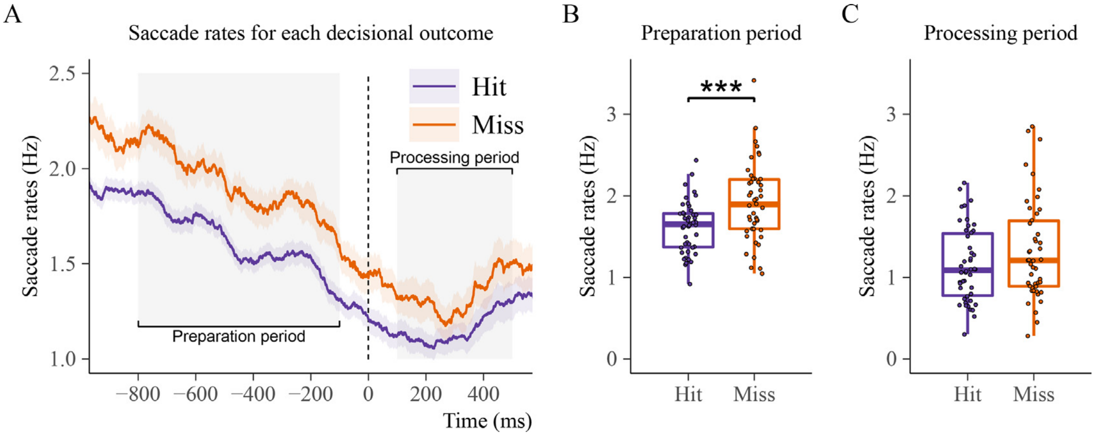

Fig. 3. Lower prestimulus saccade rates associated with better detection of short visual asynchronies. Saccade rates time-locked to the first target onset (A). Saccade rates decrease progressively as time elapses until the onset of the targets. Colored shaded areas represent one standard error of the mean. This pre-stimulus saccadic inhibition – also called oculomotor freezing – was enhanced prior the detection of asynchronies (Hits), which suggests that gaze stability helps the detection of very short visual asynchronies (B). Saccade rates did not differ between detected and undetected asynchronies after the onset of the targets (C). *** $p < .001$.

we performed a three-way mixed ANOVA on the saccade rates with the factors Response (Hit vs Miss), Group and Time-window (Anticipatory vs Processing period). As a reminder, a hit means a correct detection of an asynchrony, whereas a miss means that the participant gave a ‘simultaneous’ response despite the onset asynchrony of the target stimuli. As described in the literature (Denison et al., 2019), if the inhibition of small saccades is related to detection abilities, then the inhibition of small saccades should be more marked for hits than for misses. The analysis revealed a main effect of the Response ($F(1,44) = 34.08$, $p < .0001$; $\eta^2_{\text{partial}} = 0.437$, Fig. 3) and the Time-window ($F(1,44) = 115.62$, $p < .0001$; $\eta^2_{\text{partial}} = 0.754$). The analysis also revealed an interaction between the Response and the Time-window ($F(1,44) = 8.87$, $p = .005$; $\eta^2_{\text{partial}} = 0.168$). Saccade rates were lower during the anticipatory period of hits (Mean $_{\text{Hit}}$ = 1.62 Hz, CI $_{\text{Hit}}$ = 0.09 Hz) than of misses (Mean $_{\text{Miss}}$ = 1.92 Hz, CI $_{\text{Miss}}$ = 0.14 Hz, $p = .0006$; Fig. 3B). This effect was absent during the processing period ($p = .118$, Fig. 3C). This analysis extends previous results (Amit et al., 2019; Betta and Turatto, 2006; Denison et al., 2019) and supports the hypothesis that oculomotor freezing is associated with improved preparedness and thereby facilitates the detection of very short visual asynchronies. Importantly, this oculomotor freezing did not differ between groups ($p = .401$). Finally, a two-way mixed ANOVA with the factors Group and SOA applied to the saccade rates recorded during the processing period revealed no effect (all $p > .43$).

3.3. *Parieto-occipital alpha-band power is associated with the enhancement of perceptual sensitivity to short visual asynchronies in VGPs*

We performed a mixed ANOVA on the parieto-occipital alpha-band power with the factors SOA, Group, and Time-window (Fig. 4). The analysis revealed main effects of the Group ($F(1,44) = 6.43$, $p = .015$; $\eta^2_{\text{partial}} = 0.127$) and the SOA ($F(3,132) = 13.35$, $p < .0001$; $\eta^2_{\text{partial}} = 0.233$). Moreover, the analysis showed interaction effects between the Group and the SOA ($F(3,132) = 3.87$, $p = .011$; $\eta^2_{\text{partial}} = 0.081$), between the SOA and the Time-window ($F(3,132) = 16.75$, $p < .0001$; $\eta^2_{\text{partial}} = 0.276$) and between the Group and the Time-window ($F(1,44) = 5.58$, $p = .023$; $\eta^2_{\text{partial}} = 0.113$). In accordance with our hypothesis, the analysis revealed a triple interaction between the three factors ($F(3,132) = 3.74$, $p = .013$; $\eta^2_{\text{partial}} = 0.078$), such as the power of the parieto-occipital alpha power was reduced in VGPs compared to NVGPs during the processing of the 0 ms ($p = .0339$), 11 ms ($p = .0012$) and 33 ms SOAs ($p = .0483$) but not 66 ms SOAs ($p = .172$). These effects were absent in the preparation period (all $p > .186$). A supplemental analysis indicated that these effects were driven by evoked rather than induced alpha power (see Supplemental Materials). Similar conclusions are drawn when analyzing the amplitude of the peak of the alpha-band response (see Supplemental Materials). The latency of the peak of the alpha-band response did not differ across SOAs or groups (see Supplemental Materials). The analysis of the parieto-occipital alpha-band ITC suggest that phase coherence is an electrophysiological signature of the processing of very short visual asynchronies. Crucially, this phase coherence was reduced in VGPs relative to NVGPs (see Supplemental Materials; Fig. S5).

A correlation analysis linked the alpha-band power to the asynchrony discrimination sensitivity. Independently of the groups, the alpha-band power during the processing period and the perceptual sensitivity (d') were significantly correlated for asynchronies of 11 ms ($r = -0.355$, $p = .0155$) and 33 ms ($r = -0.316$, $p = .0322$), but not 66 ms ($p = .48$). No correlation was revealed when considering each group separately (all $p > .0998$).

The cluster-based permutation test of the source estimates indicated a significant reduction ($p < .01$) of alpha-band activations in VGPs compared with NVGPs during the 100–300 ms time window (Fig. 5). The significant cluster starts at 122 ms and finishes at 300 ms, and spreads over the left parietal and premotor cortex. Unfortunately, no strong inference can be derived from a cluster-based permutation test (Sassenhagen and Draschkow, 2019), and we will remain cautious in its interpretation. Yet, this analysis supports ITC and power analysis suggesting an effect of the group on alpha-band activities. Altogether, these analyses suggest that the enhanced perceptual sensitivity of VGPs to very short asynchronies is partially reflected in the reduction of alpha-band activities during visual processing. Notably, it is only during the processing of the targets that posterior alpha-band oscillations reflected the enhanced temporal discrimination ability in VGPs.

A series of control analyses revealed (1) no relationship between the parieto-occipital alpha-band power and the criterion (c) values, (2) no difference between groups in the midfrontal theta-band oscillatory activity – a marker of cognitive control (Cavanagh and Frank, 2014; Cohen, 2014; see Fig. S8), and (3) no difference between groups in the individual alpha frequencies (see details in Supplemental Materials).

4. Discussion

Is the ability to discriminate in time visual events enhanced in video game players? In this cross-sectional study, we evaluated the temporal discrimination abilities in vision at the millisecond level in VGPs and NVGPs using a simultaneity judgment task performed in virtual reality, while measuring EEG and oculomotor activities. During the task, par-

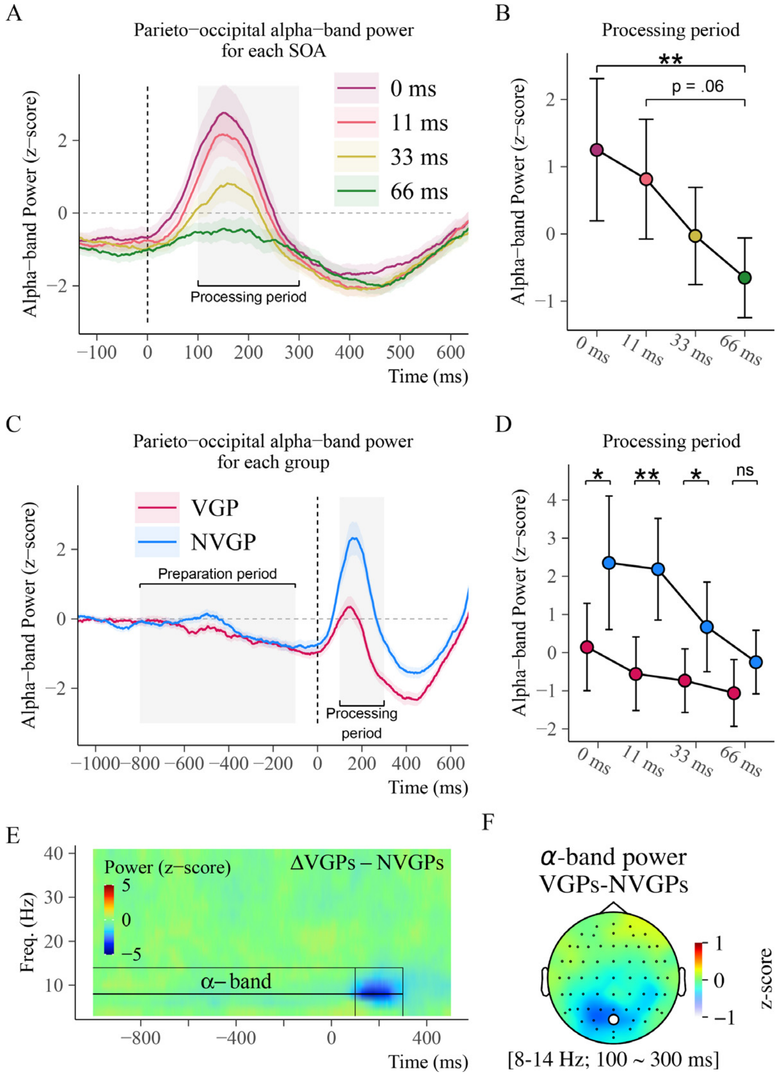

Fig. 4. Parieto-occipital alpha-band power around the onset of short visual asynchronies. Parieto-occipital alpha-band (8–14 Hz) power time-locked to the first target onset across SOAs (A). As the SOA between the two targets increases, the evoked alpha-band power response decreases (B). Both synchronous (0 ms SOA) and asynchronous targets (11 ms and 33 ms SOAs) elicited stronger alpha-band power reductions in VGPs (red) relative to NVGPs (blue) during the processing period (C-D). This difference in power values between groups was also specific to the alpha-band, the 100–300 ms time window (E) and the parieto-occipital areas (F). * $p < .05$, ** $p < .01$. Colored shaded areas represent one standard error of the mean. Error bars represent one confidence interval of the mean.

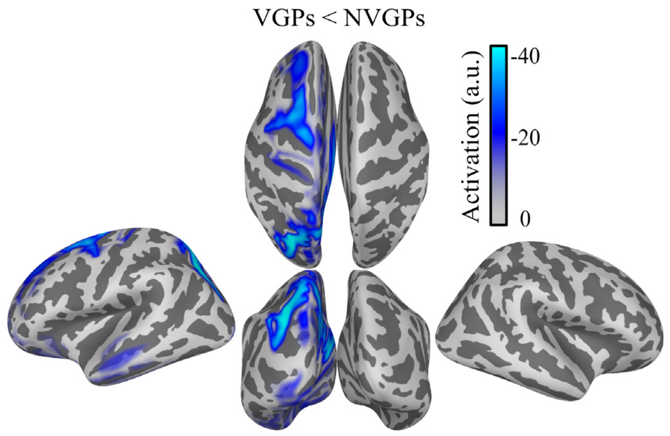

Fig. 5. Source reconstruction of the effect of the group on the alpha-band oscillations. Cluster-based permutation test of the alpha-band source estimates revealed a lower activation in VGPs compared with NVGPs within the 100–300 ms time window.

ticipants had to judge whether two targets located on the left and right visual fields appeared simultaneously or not. The asynchronies between targets were either 0 ms, 11 ms, 33 ms or 66 ms and were equiprobable. Behavioral data indicated an enhanced ability to detect visual asynchronies in VGPs. Although performance fluctuated across blocks, this enhanced ability of VGPs was observed both at the beginning and at the end of the testing protocol. Results from control analyses of reaction times and the response bias rule out the possibility of different decision-making strategies. Our results support evidence that the improved ability of VGPs is not observed only with multisensory targets but also in the unisensory visual modality. Indeed, in another SJ task, VGPs were better at detecting asynchronies between visual and auditory stimuli (Donohue et al., 2010). The results of Donohue et al. (2010) might have been specific to the use of audiovisual targets. Our results generalize their findings and suggest that it is temporal discrimination skills that are improved rather than mechanisms specific to multisensory processing. Furthermore, the recording of saccades and EEG help to dissociate the role of preparatory and target processing mechanisms. On the one hand, control measures showed that pre-target oculomotor freezing – the inhibition of small fixation saccades – facilitated the detection of asynchronies. Yet, this oculomotor freezing did not explain the advantage of VGPs. On the other hand, the power and phase coherence of occipito-parietal alpha-band oscillations recorded during target processing differed between VGPs and NVGPs, providing a neurophysiological correlate for the enhanced temporal discrimination abilities in VGPs. All evidence suggests that perceptual rather than preparatory mechanisms explain the improved performance in VGPs. More precisely, the superior ability of VGPs in discriminating rapidly presented visual events in time is, at least in part, related to an altered parieto-occipital functioning. It is to be noted that this pathway does not mean a purely sensory mechanism. Perceptual mechanisms mean here processes that occur after the display of the targets. They involve both feed-forward mechanisms and top-down attention modulation. Overall, the data suggest an increased temporal resolution of vision in VGPs.

According to the learning-to-learn account (Bejjanki et al., 2014; Green et al., 2010; Zhang et al., 2021), VGPs excel in a variety of tasks due to an enhanced ability to learn the variables relevant to the task at hand. We did not find conclusive evidence supporting this hypothesis. The learning-to-learn account would have predicted a faster pace of performance improvement over time in VGPs than NVGPs, which is not the case here. While the performance of NVGPs first improves over the course of the study, the performance of VGPs is rather deteriorating. In fact, VGPs were better than NVGPs at detecting the asynchronies especially during the very first trial block. This suggests the performance of VGPs was at best at the start of the task, whilst NVGPs required some practice to improve their performance. Our results do not rule out the learning-to-learn account, though, as the number of to-be-detected SOAs was only four: the training phase may have been enough to adjust a strategy. The attentional control account (for a review see Bavelier and Green, 2019) suggests that action video game play enhances the capacity to shift between attention modes based on task demands. Here, neither response bias (*c* values) nor midfrontal theta power, a marker of cognitive control (Cavanagh and Frank, 2014; Cohen, 2014), substantially differed between VGPs and NVGPs, thus suggesting similar cognitive strategies to perform the task. While the present results seem challenging both the learning-to-learn and attention control accounts of video game-based enhancements, additional evidence is required to rule out the involvement of these mechanisms in the enhancement of temporal discrimination in VGPs. Detecting asynchronies that are near the threshold is a demanding task, and it is possible that gamers allocated attention more efficiently in time when processing the asynchrony (but not when preparing to process the targets).

Whatever the mechanisms at play, the results suggest the possibility of a transfer learning effect. In the case of video games, the fast-paced visuomotor experience through gaming might facilitate the processing of rapidly presented visual targets in other tasks (Donohue et al., 2010; Pohl et al., 2014; West et al., 2008). Such a transfer effect could be at play here. Action video games may improve visuo-temporal skills that are essential to other tasks, including the SJ task. Traditional learning paradigms showed that the ability to detect visual (Virsu et al., 2008) and auditory (Mossbridge et al., 2006) asynchronies can be trained through practicing computer-based tasks specifically designed to train the detection of asynchronies. Our results suggest that the ability to detect asynchronies is enhanced in VGPs, even though action video games do not explicitly train players in this cognitive feature. Interventional studies will be required to evaluate the causal relationship between the enhancement of temporal discrimination skills and action video game play.

Recent work showed that visual attention is associated with anticipatory decreases in small oculomotor movements (Weaver et al., 2017). Through attention, the temporal anticipation of targets induces oculomotor freezing (Abeles et al., 2020; Amit et al., 2019; Badde et al., 2020). First, the present study replicates prior data showing that oculomotor freezing can be extracted from a VR setup (Foerster et al., 2022). Second, our results show that oculomotor freezing is associated with better discrimination in time of fast stimulus onset asynchronies across the visual field. This could reflect an optimal sampling strategy of the visual system to differentiate forthcoming signals (Martinez-Conde et al., 2009) and 'be ready' to process rapid changes across the visual space. This strategy would be in accordance with the general idea that oculomotor freezing promotes visual perception (Martinez-Conde et al., 2006). The importance of anticipatory preparation in timing is widely accepted, at least for sequences above 100 ms (Nobre and van Ede, 2018), and the present results are consistent with results suggesting the existence of such mechanisms at the level of milliseconds (Marques-Carneiro et al., 2021). However, this oculomotor freezing appeared to be similar in VGPs and NVGPs. Likewise, the analysis of the pre-target alpha-band oscillations did not show differences between groups. Thus, both eye-tracking and EEG data rule out the hypothesis of different preparatory mechanisms in VGPs and NVGPs. Such results may appear in contrast with the proposal that video game experience affects proactive rather than reactive control of visual processing (Bailey et al., 2010). However, impaired proactive control was observed when using a Stroop task, and not a demanding perceptual discrimination task. The task differences may explain the discrepancy. Besides, these results also suggest that overt recruitment of gamers did not affect how they mobilized preparatory mechanisms, showing that the observed effects are not due to a generalized improvement.

Alpha-band oscillations have been associated with many perceptual and cognitive functions (Clayton et al., 2018). Our data suggest that VGPs outperformed NVGPs in a visual SJ task. It is only during the processing of asynchronies that alpha-band oscillations differed between groups. How could a reduction of alpha-band response facilitate the detection of very short asynchronies? Several proposals argued that alpha-band power reflect states of increased neuronal excitability (Iemi et al., 2017; Klimesch et al., 2011, 2007) which, in turn, increases the decisional bias (leading to a more liberal decision criterion) and/or increase the perceptual sensitivity to the stimuli. However, recent findings challenge this model and rather suggest that alpha power reflects the gating of neuronal activities in downstream regions to modulate feed-forward information processing (Gundlach et al., 2020; Zhigalov and Jensen, 2020). Previous studies on visual attention showed increase of alpha-band power in the to-be-ignored location and decrease of power in the to-be-attended location (e.g. Gundlach et al., 2020; Popov et al., 2017; Thut et al., 2006). This might generalize to temporal processing, and a possibility is that the present alpha-band alterations found in VGPs could reflect a particular neuronal gating mechanism facilitating feed-forward processing of incoming information from lower visual areas in a top-down manner.

In this experiment, the decisional bias does not differ between groups. Moreover, the decrease of alpha power was associated with an increased sensitivity to the asynchronies. However, this was true when considering all participants. These correlations were not significant within groups. Also, no relation between the alpha power and the decisional bias was reported. Finally, the fact that VGPs exhibit reduced alpha-band responses to 0 ms, 11 ms and 33 ms SOAs, but not 66 ms SOA, compared to NVGPs fits with the idea of improved discrimination abilities rather than different reactions to asynchronies. Altogether, the data suggest that the enhanced temporal discrimination skills in VGPs rely on altered processing states in parieto-occipital areas, and may rely on improved allocation of attention in time when the asynchrony is short (Coull and Giersch, 2022; Coull and Nobre, 1998).

Our results are in line with previous studies suggesting that post-stimulus alpha-band power decrease is associated with improved detection of rapidly presented visual stimuli (Babiloni et al., 2006; Brüers and VanRullen, 2018; Ergenoglu et al., 2004; Klimesch, 1999; Trafton et al., 2013) and improved speed of visual information processing (Hilla et al., 2020). Similar to Hilla et al. (2020), the results show a reduction of the alpha-band power in VGPs. Recent work showed that increases in alpha-band power facilitate complex visual feature binding (Zhang et al., 2019), which in our task may be related to increased alpha-power when the SOA is 0 ms. Conversely, one could speculate that the decrease in alpha-band power in VGPs during temporal discriminability may facilitate visual partitioning in time. Future investigation will be required to test such a hypothesis.

5. Conclusion

Brain plasticity is the favored scientific explanation for the cognitive enhancement induced by video game play (Bavelier et al., 2012). Yet, the characteristics of this brain plasticity remain unknown. Here, data suggests that altered states in parieto-occipital areas facilitate the ability to discriminate in time one visual event from another. The enhanced task performance in VGPs also suggests that playing action video games could induce changes in temporal discrimination at the millisecond scale. Hence, temporal discrimination skills could be improved without being specifically trained to do so. Importantly, future interventional studies are required to verify this hypothesis. Other limitations are the absence of control of the potential influence of feeling of immersion and prior experience with VR on the task. Finally, the education level was slightly higher in VGPs in the present study, but the small difference between the groups unlikely explains the results. Importantly, our samples were gender-balanced, even though the low number of included females prevented us from performing an analysis of gender effect (Buono et al., 2020). Our results support the idea that video games could represent a remediation tool in clinical populations (Shams et al., 2015), especially people with schizophrenia (Giersch et al., 2009; Lalanne et al., 2012; Marques-Carneiro et al., 2021) and autism spectrum disorders (Falter et al., 2012) whose processing of visual asynchronies appeared defective. While previous research demonstrated that action video game play improves the spatial resolution of vision (Li et al., 2009), the present data suggest an enhancement of the temporal resolution of vision in action video game players.

Data availability

Codes and data are available in the open science framework and accessible at https://osf.io/geqz4/.

Credit authorship contribution statement

Francois R Foerster: Conceptualization, Data curation, Formal analysis, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Matthieu Chidharom:** Writing – review & editing. **Anne Giersch:** Funding acquisition, Project administration, Supervision, Conceptualization, Writing – review & editing.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2023.119906.

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