RESEARCH REPORT

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Shift in lateralization during illusory self-motion: EEG responses to visual flicker at 10 Hz and frequency-specific modulation by tACS

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Abstract

Self-motion perception is a key aspect of higher vestibular processing, suggested to rely upon hemispheric lateralization and alpha-band oscillations. The first aim of this study was to test for any lateralization in the EEG alpha band during the illusory sense of self-movement (vection) induced by large optic flow stimuli. Visual stimuli flickered at alpha frequency (approx. 10 Hz) in order to produce steady state visually evoked potentials (SSVEPs), a robust EEG measure which allows probing the frequency-specific response of the cortex. The first main result was that differential lateralization of the alpha SSVEP response was found during vection compared with a matched random motion control condition, supporting the idea of lateralization of visual–vestibular function. Additionally, this effect was frequency-specific, not evident with lower frequency SSVEPs. The second aim of this study was to test for a causal role of the right hemisphere in producing this lateralization effect and to explore the possibility of selectively modulating the SSVEP response. Transcranial alternating current stimulation (tACS) was applied over the right hemisphere simultaneously with SSVEP recording, using a novel artefact removal strategy for combined tACS-EEG. The second main result was that tACS enhanced SSVEP amplitudes, and the effect of tACS was not confined to the right hemisphere. Subsequent control

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experiments showed the effect of tACS requires the flicker frequency and tACS frequency to be closely matched and tACS to be of sufficient intensity. Combined tACS-SSVEPs are a promising method for future investigation into the role of neural oscillations and for optimizing tACS.

1 | INTRODUCTION

The unified perception of body position and self-motion requires the integration of information from the vestibular system with visual and somatosensory input; the processes underlying this integration are lateralized to the non-dominant hemisphere (Arshad, 2017; Dieterich & Brandt, 2015, 2018). Studies using several imaging and stimulation techniques have shown a dominance within the vestibular cortical network of the right hemisphere in right-handers and of the left hemisphere in left-handers (Dieterich et al., 2003; Janzen et al., 2008; Zu Eulenburg, Caspers, Roski, & Eickhoff, 2012). Imaging studies show activation in parietal regions in response to vection, the illusion of self-motion (Brandt, Bartenstein, Janek, & Dieterich, 1998; Kaski et al., 2016; Kleinschmidt et al., 2002), and lesions of the right hemisphere are more frequently related to disorders such as visuo-spatial hemineglect which may be relevant to higher vestibular cognition (Brandt, Strupp, & Dieterich, 2014; Karnath & Dieterich, 2006). Recent evidence implicates dorsal areas, including the parietal cortex, in multisensory visual–vestibular processing such as in determining heading or slant (Avila, Lakshminarasimhan, DeAngelis, & Angelaki, 2019; Elmore, Rosenberg, DeAngelis, & Angelaki, 2019; Willacker, Dowsett, Dieterich, & Taylor, 2019).

Vection can be induced by presenting visual optic flow and involves a temporary mismatch between vestibular and visual information. EEG studies (Palmisano, Allison, Schira, & Barry, 2015) have found an increase in alpha activity during optic flow (peaking 14 s after stimulus onset) which correlated with stronger vection ratings (Palmisano, Barry, De Blasio, & Fogarty, 2016), although other studies have found alpha de-synchronization from optic flow for short (1 s) display times (Vilhelmsen, van der Weel, & van der Meer, 2015). Research into visual responses using EEG and actual body movement has found a suppression of alpha power (Ehinger et al., 2014; Gale et al., 2016; Gutteling & Medendorp, 2016). A common conclusion among these studies is that alpha power modulations are related to vestibular processing and self-motion estimates.

Although the exact function of alpha oscillations is a topic of active research, the dominant hypothesis is that alpha-band oscillations serve as a mechanism for rhythmic inhibition (Van Diepen, Foxe, & Mazaheri, 2019). Traditionally, alpha oscillations have been thought of as the inhibition of task-irrelevant regions, whereas some theories suggest alpha oscillations reflect a more directly functional role in gating and facilitating the transfer of information. There are a number of ways in which these proposed roles of alpha oscillations could mediate visual–vestibular interactions: firstly as a gating mechanism to integrate modality-specific inputs arriving from distant neural areas. This fits with the idea that coherence of oscillatory neural signals is critical for multisensory perception (Keil & Senkowski, 2018; Senkowski, Schneider, Foxe, & Engel, 2008). Secondly, alpha oscillations could reflect the inhibition of movement in the visual field due to self-motion, in line with a general role for alpha-band oscillations in suppression and selection of attention and the ability to be consciously oriented in time and space (Klimesch, 2012).

There is, however, scant evidence bridging the concepts of lateralization of higher vestibular function and alpha responses underlying vection. The current study hypothesized that during vection, there would be greater lateralization of the EEG response than during a control condition without vection. Such lateralization would be consistent with the overarching idea of the lateralization of higher vestibular function, including multisensory processes related to navigation (Dieterich & Brandt, 2015, 2018). Although alpha lateralization during vection may not have been explicitly tested for in the past, lateralization of alpha (and other frequency bands) is apparent in human intracranial recordings during virtual reality navigation (Jacobs et al., 2010). Some of the components derived from event-related spectral perturbation analysis during vection show lateralization (Palmisano et al., 2016), and it has been suggested that lateralization in the alpha band may be important during postural control (Edwards, Guven, Furman, Arshad, & Bronstein, 2018).

Observing neuronal oscillations in response to various stimuli implies a functional role but this evidence is only correlational: to demonstrate a causal effect of neural oscillations and to develop frequency- targeted clinical interventions, direct manipulation of the oscillations is required (Herrmann,

Strüber, Helfrich, & Engel, 2016). Here, cortical activity in response to vection induced by optic flow was investigated by combining two techniques which both modulate (or generate) neuronal oscillations in a frequency-specific manner: steady state visually evoked potentials (SSVEPs) and transcranial alternating current stimulation (tACS).

Steady state visually evoked potential research paradigms (Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015) typically involve various elements on a display flickering at one or more frequencies which can be measured in the EEG signal. SSVEPs can be seen in the EEG at frequencies ranging from 1 to 100 Hz, but show higher amplitudes in resonant frequency bands (alpha, beta, gamma etc.) due to an interaction with the preferred frequency of endogenous neural oscillations in the cortex (Herrmann, 2001). The high signal-to-noise ratio, and the ability to probe specific frequency bands, makes SSVEPs an appealing method, but to fully understand and exploit this potential the ability to selectively modulate these responses is desirable.

Transcranial alternating current stimulation (tACS) involves stimulating the cortex with a weak current via electrodes attached to the scalp at frequencies matching functionally relevant neural oscillations to entrain or modulate ongoing brain activity. An increasing number of studies have demonstrated frequency-specific effects of tACS in humans (e.g. Feurra et al., 2011; Wach et al., 2013), and these effects are thought to be due to the frequency of the stimulation being close enough to the oscillating neural activity that entrainment can occur (Herrmann, Rach, Neuling, & Strüber, 2013).

Transcranial electrical stimulation generally has a huge potential as a research tool and clinical intervention but suffers from low power and variability across individuals. A primary goal of this study was to find an effect which can be seen at the individual subject level which can be used to individualize and optimize the many stimulation parameters in future research. Closely matching the frequency of stimulation to a neural oscillation is a promising strategy for maximizing the effect of tACS.

However, endogenous neural oscillations do not occur at precise frequencies, they can shift frequency over time, vary significantly across individual, and the phase can be reset by external stimuli. SSVEPs, on the other hand, occur at the exact frequency of the driving visual flicker, and the phase remains constant relative to the visual stimulus, offering the combination of tACS and SSVEPs greater utility than either alone. This could potentially be a particularly useful experimental paradigm as the frequency and phase of the evoked neural oscillations relative to the tACS can be precisely controlled and thus targeted with greater efficacy (Chai, Sheng, Bandettini, & Gao, 2018; Ruhnau, Keitel, Lithari, Weisz, & Neuling, 2016).

In the current study, two visual stimuli (optic flow and random dot movement) were used, matched for low-level visual properties as a cognitive control to investigate any state-specific effects of tACS. The goals of the current study were, firstly, to investigate the potential of SSVEPs to probe cortical visual–vestibular interactions and hemispheric lateralization during vection; secondly, to investigate the ability of tACS to modulate this oscillatory response in a hemisphere-specific way; and thirdly, to find a reliable effect of tACS on frequency-matched SSVEPs with the aim of optimizing stimulation protocols in future research. To this end, a series of control conditions were included to demonstrate that tACS at nearby flanker frequencies, or at low amplitudes, does not have a significant effect on SSVEPs.

2 | METHODS

2.1 | Overview

Steady state visually evoked potentials were utilized to probe the response of the cortex to optic flow, in particular the relative responses of left and right hemispheres in the alpha range to test for hemispheric dominance of visual–vestibular interaction. To target the role of alpha-band oscillations in the right hemisphere, tACS was applied with a right lateralized montage to healthy right-handed volunteers. Participants were shown flickering optic flow stimuli and a control condition of random dot movement, whilst standing. Stimuli were projected with a large visual angle (90°). Participants were asked to report feelings of vection, whilst EEG was recorded online, both during stimulation and in a baseline condition. All participants received an identical baseline condition and an identical condition in which 1 mA tACS (2 mA peak to peak) was matched closely to the flicker frequency. In addition, three control conditions were administered to demonstrate that the effect of the tACS was exclusive to 1 mA frequency-matched stimulation: the first 10 participants received tACS at two flanker frequencies, the next 10 received frequency-matched tACS at various lower intensities, and in a separate experiment a flicker frequency control.

2.2 | Participants

The first experiment was conducted on 20 participants, and the second experiment was conducted on 10 participants drawn from the same sample. Participants had a mean age of 26.5 years (range 22–33). All participants self-reported as right handed and were tested on the Edinburgh handedness inventory (100 = fully right handed, −100 = left handed and 0 = ambidextrous); mean score was 80.25 (range 33–100).

The study was approved by the local ethics committee (LMU Medical Faculty). All participants had the experimental procedure explained to them, gave signed informed consent and were free to withdraw from the experiment at any

time. One participant asked to withdraw from the experiment because the optic flow stimulus was causing motion sickness; this subject was not included in the final analysis and was replaced by another.

2.3 | Stimuli

Stimuli consisted of two movies: optic flow dot pattern and a random dot motion control. Movies were created in MATLAB (The MathWorks Inc., Natick, MA, USA) using the Psychtoolbox extension. Stimuli consisted of white dots on a black background with a central fixation cross. Optic flow movies were created by first assigning a random position in 3D space to a large number of dots, and the correct size and position of each dot from the perspective of the observer was calculated and converted to a screen position for each frame of the movie. The position of the observer was moved through space; this recreated the key features of true optic flow: object looming, acceleration towards the peripheral of the field of view, motion parallax etc. The random control movie consisted of the same number of dots as were on the screen in any one frame of the optic flow condition, and the size of the dots was kept constant such that the number of white pixels on the screen (and therefore the total luminance) was on average the same as the optic flow movie. The dot motion was in a random direction for each dot, and the speed was set to the average screen speed of the dots in

the optic flow movie (approx. 15 degrees per second). In addition to the central fixation cross, a grey circle of approximately two degrees visual angle was in the centre of the screen during each movie to occlude any dots moving across the fixation point (2 degrees approximately corresponds to the fovea).

To evoke SSVEPs, a flicker was introduced to the movies by darkening the white dots (to middle grey) for two consecutive frames out of every six frames; this value was chosen to minimize the saliency of the flicker whilst still evoking a reliable SSVEP. If the refresh rate of the projector were exactly 60 Hz, this would result in a 10 Hz flicker; most '60 Hz' displays actually run at slightly slower than 60 Hz by design (59.97 Hz); in our case, the true refresh rate (as measured with Psychtoolbox and external triggers sent with each frame) was approximately 59.89 Hz giving a flicker of approximately 9.98 Hz. As such, 10 Hz tACS and approximately 9.98 Hz flicker is a convenient method for presenting two nearby frequencies. We used this fact in our experimental design as we wanted the visual flicker to slowly drift in and out of phase with the 10 Hz tACS such that over the course of the experiment all relative phases were present, to maximize the likelihood of hitting the optimal phase (which may be different for each individual). Delivering the tACS at exactly the same frequency as the visual flicker would result in only one relative phase between the stimulation and the SSVEP, which may be suboptimal or have no effect at all. The fixation cross and central circle did not flicker.

Optic flow or random dot motion flickering at 9.9 Hz 5 seconds

Fixation cross 3 seconds

Vection sensation response 2 seconds

10 second trial repeated 6 times for each block of 1 minute

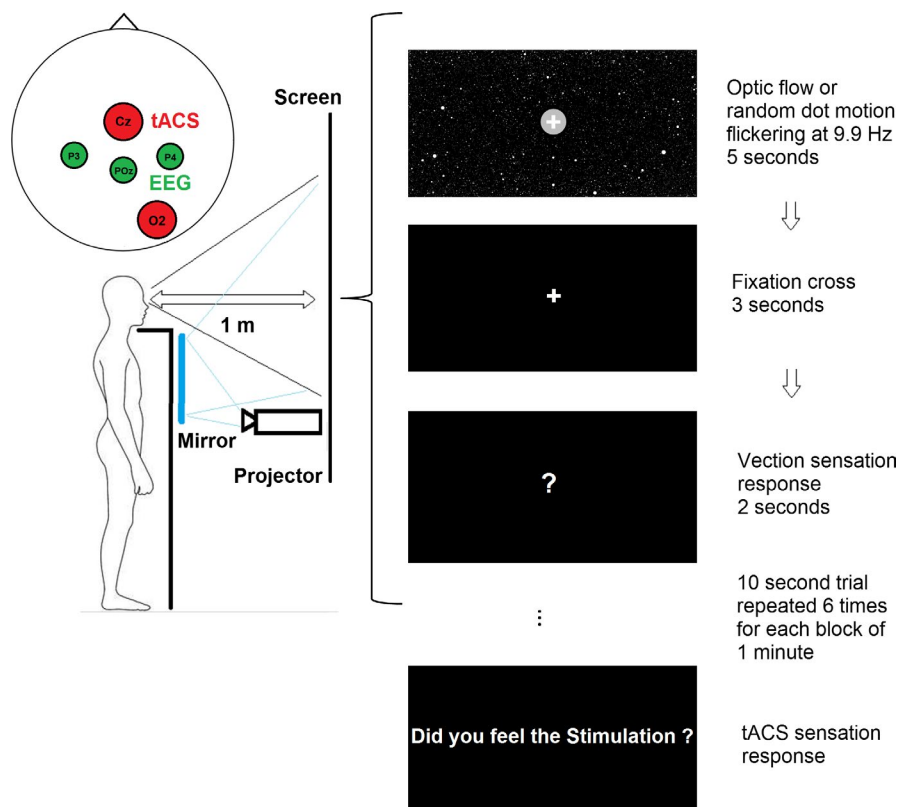Did you feel the Stimulation ?

tACS sensation response

FIGURE 1 Experimental set-up and procedure [Colour figure can be viewed at wileyonlinelibrary.com]

2.4 | Experimental design

Participants were standing for the duration of the experiment; this was done to maximize the feeling of vection and to minimize any tactile clues that would be present if sitting. Standing, as opposed to sitting, has been reported to be associated with longer vection durations but not vection onset latencies (Guterman, Allison, Palmisano, & Zacher, 2012); however, our pilot data indicate this set-up is able to produce feelings of vection within 5 s in most participants (see results). Viewing distance was one metre in front of a projection screen with the head supported by a chinrest. The display was projected (LCD projector, Epson) onto the screen using a mirror to increase the size of the display (see Figure 1). This was done to allow the size of the display to be 90 degrees of visual angle in the horizontal plane and approximately 73° in the vertical plane. The experiment was performed in a darkened room with the projector being the only source of light. Participants were instructed to fixate on the central cross throughout.

In each experiment, participants were shown the stimuli in 24 blocks; each block contained six movies: three of optic flow and three of random dot motion, in randomized order. Each movie was five seconds long, followed by three seconds of a blank screen with a fixation cross, followed by a question mark prompting the subject to report their sensation of vection. Participants had two seconds to respond making a ten second trial, which was repeated six times to make a one minute block (i.e. participants had to keep in memory their experience of vection and respond after 3 s). The 24 blocks were randomly allocated into one of four stimulation conditions giving six blocks for each condition. Responses were manual button presses using one of four buttons on a custom-built response box, corresponding to the following: No vection, weak vection, moderate vection and strong vection. At the end of each one minute block, after the last vection response, participants were asked whether they felt the tACS stimulation and if so how strong the sensation was compared with a short period of stimulation given at the beginning of the experiment (2 mA peak to peak), and participants responded with the same four buttons indicating: no sensation, weaker/faint sensation, same as when they first felt the stimulation, stronger sensation (0 = no sensation, 1 = less, 2 = same and 3 = more). This was done to compare the sensations across conditions and to track how the sensation of tACS diminishes over time.

Participants were allowed to take short rests between blocks if requested. At the end of the experiment, the participants filled out an additional questionnaire reporting their overall feeling of vection during the experiment for the two conditions (as a percentage from 0% to 100%, with 100% indicating strong vection, i.e. 'it felt as if I was really moving' and 0% indicating no feeling of vection). In addition, participants were asked about any feeling of motion sickness, any adverse effects of the stimulation and whether they perceived any phosphenes (it was made clear that this was not the flickering screen but due to the stimulation when there was no visual flicker).

2.5 | Transcranial alternating current stimulation

Electrical stimulation was applied with two circular silicon electrodes 4 cm in diameter each, placed at positions Cz and O2 (Neuroconn Multi-channel stimulator, Munich, Germany). Cz and midline electrode *Oz* (not right hemisphere O2) have been used in a number of tACS experiments as modelling studies indicated that this montage is optimal for current reaching parietal lobes (Neuling, Wagner, Wolters, Zaehle, & Herrmann, 2012). In the current study, we placed the occipital electrode at O2 to bias the current flow towards the right hemisphere. Stimulating electrodes were attached using a conductive paste, and the impedance was measured to ensure it was below at least 10 kOhms.

Both experiments consisted of four stimulation conditions; the order was randomized in all experiments. For the first 10 participants, the four conditions were as follows: tACS at 10 Hz, 8.3 Hz and 12.5 Hz (all at 1 mA, 2 mA peak to peak) and a baseline condition where the stimulation was switched off (no tACS). Participants 11–20 (intensity control) received three different tACS intensities: 0.1 mA (0.2 mA peak to peak), 0.5 mA (1 mA peak to peak) and 1 mA (2 mA peak to peak), all at 10 Hz and a baseline condition. The second experiment consisted of two baseline conditions, one with the visual stimulus flickering at 9.9 Hz (as in the first experiment) and one with an approximately 8.6 Hz flicker (achieved by darkening two frames out of every 7), and two tACS conditions consisting of the two flicker frequencies with 10 Hz tACS at 1 mA (2 mA peak to peak). This control experiment was intended to both test whether there is an interaction between optic-flow/random movement and flicker frequency being closer or further from typical alpha frequency (10 Hz), as well a control to demonstrate that removing a 10 Hz tACS artefact does not corrupt SSVEPs at other frequencies.

In a recent study, we applied tACS using various 'sawtooth' waves in addition to the traditional sinusoidal waveform (Dowsett & Herrmann, 2016); waveforms such as square waves and sawtooth waves, which contain sudden transitions in current, may be more effective at influencing or entraining neuronal oscillations, but they have an additional advantage in that the distinct properties of sawtooth waves, that is, consisting of straight lines with a steep transition, do not occur in nature and are more easily distinguishable from neural activity. This makes removing the artefact from the EEG recording simpler (see below). As positive
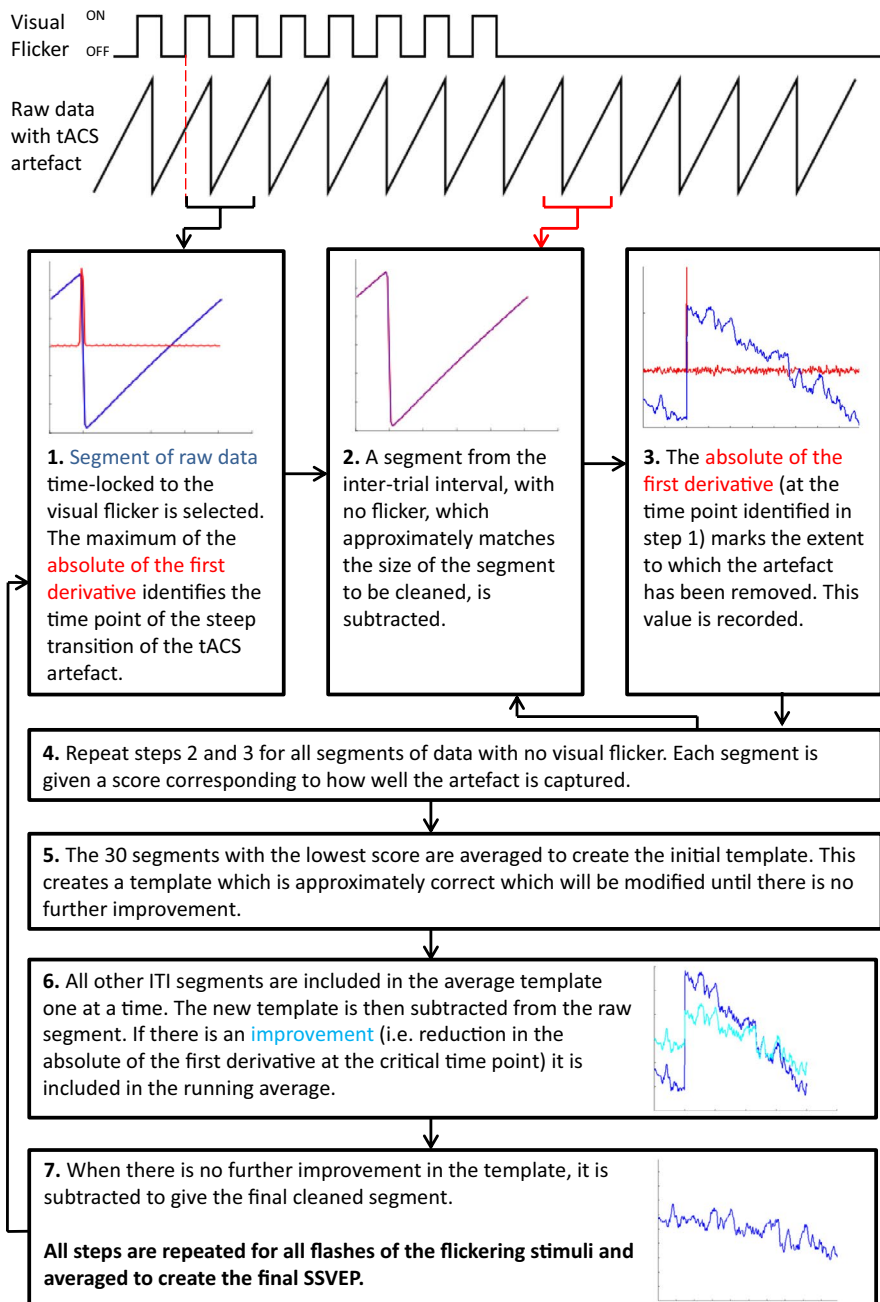
Artefact removal procedure

Visual Flicker ON OFF

Raw data with tACS artefact

1. Segment of raw data time-locked to the visual flicker is selected. The maximum of the absolute of the first derivative identifies the time point of the steep transition of the tACS artefact.

2. A segment from the inter-trial interval, with no flicker, which approximately matches the size of the segment to be cleaned, is subtracted.

3. The absolute of the first derivative (at the time point identified in step 1) marks the extent to which the artefact has been removed. This value is recorded.

4. Repeat steps 2 and 3 for all segments of data with no visual flicker. Each segment is given a score corresponding to how well the artefact is captured.

5. The 30 segments with the lowest score are averaged to create the initial template. This creates a template which is approximately correct which will be modified until there is no further improvement.

6. All other ITI segments are included in the average template one at a time. The new template is then subtracted from the raw segment. If there is an improvement (i.e. reduction in the absolute of the first derivative at the critical time point) it is included in the running average.

7. When there is no further improvement in the template, it is subtracted to give the final cleaned segment.

All steps are repeated for all flashes of the flickering stimuli and averaged to create the final SSVEP.

ramp sawtooth waves (and not negative ramp sawtooth) were previously found to enhance alpha oscillations during stimulation (Dowsett & Herrmann, 2016), this waveform was chosen for the current experiment.

2.6 | Electroencephalogram

Electroencephalogram was recorded from three electrodes at positions P3, POz and P4 on the 10/20 system, plus an EOG under the right eye (Ag/AgCl electrodes, BrainCap, Brain Products, Munich, Germany). These electrode positions are at the approximate midline between the stimulating electrodes where the stimulation artefact is smallest and unlikely to reach the limits of the range of the EEG amplifier and saturate the signal. EEG was amplified using a BrainAmp DC amplifier (Brain Products, Munich, Germany). Impedance of the EEG electrodes was kept below 5 kOhms and was recorded with a sampling rate of 5,000 Hz. The EEG was recorded with the reference on the right ear lobe and re-referenced offline to the average of two electrodes on each ear. The ground electrode was positioned on the forehead at electrode position Fpz.

2.7 | Artefact removal

The electrical artefact introduced to the EEG recording during stimulation can be several orders of magnitude larger than signals from ongoing neural oscillations and needs to be removed before the data can be analysed. The majority of simultaneous tACS and EEG/MEG studies to date have removed the artefact with either beamforming (Neuling et al., 2015) or a combination of template subtraction and principal components analysis (Helfrich et al., 2014). However, each of these methods carry their own advantages and disadvantages and some researchers have documented how modulations in the size of the artefact due to heartbeat and breathing can result in residual artefacts which can easily be confused with entrained neural activity (Noury, Hipp, & Siegel, 2016; Noury & Siegel, 2018).

Here, we present a modified 'adaptive template subtraction' method (summarized in Figure 2) which improves on the artefact removal in previous studies. Data were first segmented into 121 ms segments time-locked to 10 ms before the onset of each flash of the visual flicker. This length of time was chosen so that every segment during the tACS conditions contained at least one full cycle for all stimulation frequencies (8.3 Hz tACS has a period of 120 ms). For each stimulation block, the tACS was on for the entire time meaning the artefact was present both during the flickering stimulus and the inter-trial interval (ITI). For each flicker segment containing a tACS artefact, a template was constructed by averaging matching segments from the ITIs from the same stimulation block. This ensured that the SSVEP would not be included in the template and would not be subtracted. In addition, this ensures that any neural activity induced directly by the tACS, such as neural responses to peripheral nerve stimulation (Asamoah, Khatoun, & Laughlin, 2019) or retinal stimulation (Kar & Krekelberg, 2012), would also be included in the average template and subtracted, leaving only the SSVEP. Previous template subtraction approaches

have used a simple sliding average approach (Helfrich et al., 2014); however, due to changes in the size or phase of the artefact an incorrectly sized template can easily result in a residual artefact. Since the stimulator always tries to deliver a constant current, whenever the impedance changes the voltage will adapt and the size of the artefact in the EEG will change; changes in impedance can be due to a gradual drift in impedance from the conductive paste warming, participant movement or sweating as well as changes due to heartbeat and breathing (Noury et al., 2016). Rather than blindly creating a template, segments were selected which, when averaged, best matched the sawtooth artefact of the segment to be cleaned. This greatly increases the number of segments in which no evidence of a residual artefact can be observed compared with the simple sliding average approach used in previous studies (Dowsett & Herrmann, 2016). Specifically, the time point of the steep transition from anode to cathode in the sawtooth wave was identified and the absolute of the first derivative (i.e. the gradient) of the cleaned segment was minimized for 2 ms around this time point. The *absolute* of the first derivative was used as the residual artefact could be reversed in polarity depending on whether or not the template being subtracted is slightly bigger or smaller than the artefact in the segment being cleaned. A steep gradient at this time point would be the clearest evidence of a residual artefact; sinusoidal tACS would not contain any such steep gradients, and it is much harder to identify a residual artefact. Importantly, only this time range was used and not the entire segment which could potentially lead to over-fitting the template to the evoked response; if the template were optimized to result in the smallest overall amplitude across the entire segment, then neural activity could also be included in the template and subtracted. For each segment to be cleaned, first the 30 best segments from the surrounding ITIs were selected (i.e. segments that when subtracted from the segment to be cleaned gave the lowest value in the first derivative at the critical time point). Next, 100 additional segments from the
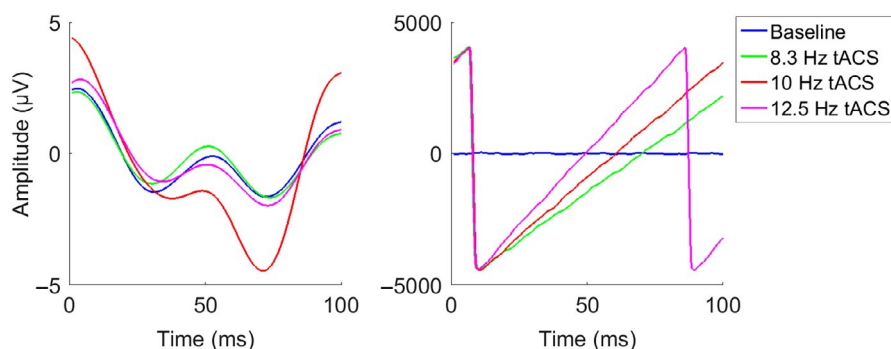

FIGURE 3 Left: Example SSVEPs from one participant from experiment 1 from electrode POz, Right: corresponding example segments of raw data from the same electrode before artefact removal. Of note is the overall similarity of SSVEP waveform and amplitudes between baseline and flanker frequency (8.3 Hz and 12.5 Hz) conditions despite the large artefact having been removed. Segments of 10 Hz tACS (red) would be no more likely to leave a residual artefact than the flanker frequencies [Colour figure can be viewed at wileyonlinelibrary.com]

surrounding ITI were considered in turn, included in the average template and subtracted from the segment to be cleaned: if there was an improvement, then the segment was included in the optimal 'running average' template, and then, the next potential segment was considered. This was repeated for up to 100 segments; when more than 100 segments are averaged to create a template, very little additional improvement can be seen. Once the optimal template had been found, this was then subtracted from the original raw segment to produce the final cleaned segment of data. This procedure was performed separately for each and every segment of data (Figure 2). Artefact removal was performed separately for each electrode, as the artefact can be significantly different across electrodes, and is not necessarily exactly the same phase.

A significant advantage of this artefact removal method is that it is no less likely to be successful across the 8.3 Hz, 10 Hz and 12.5 Hz conditions. The only input is 121 ms of data (Figure 3, right panel); the algorithm simply matches segments from the inter-trial interval to construct the template, and this is done separately for each segment of experimental data. This template matching is no more likely to be successful with 121 ms of data during 10 Hz tACS than with any other frequency, because only the steep gradient at the critical time point is being considered to determine whether template matching is successful, and it is therefore 'blind' as to the frequency of the artefact. This also overcomes some of the problems that can arise from removing the artefact from longer segments such as 'side band' artefacts in the FFT where an amplitude-modulated artefact can appear as two peaks at neighbouring frequencies (Noury et al., 2016).

As only a short segment is being cleaned at any one time, it is more likely that a correctly matching segment can be found: if the artefact is being removed from longer periods (e.g. 1 s), the artefact might have changed in size far more in that time and it is less likely that a correctly matching template can be constructed. Variations in the artefact due to breathing and heartbeat do not occur at the flicker frequency and are removed by averaging enough short segments, as demonstrated by the lack of effect in the control conditions (see results).

A further advantage of sawtooth waves (or square waves) over sine waves is that small differences in the phase of the artefact and the template result in large residual artefacts when the template is subtracted and are immediately obvious (see Figure 9); unless the phase exactly matches the segment, it will not be included in the template. This is not the case for sine wave artefacts where small differences in the phase can result in small residual sinusoidal artefacts which cannot easily be distinguished from neural oscillations (see discussion).

2.8 | EEG Data analysis

After tACS artefact removal, any segments containing eye blinks or movement artefacts were rejected (range greater than 50 µV in EOG channel or 200 µV in the segment itself), and the remaining segments of data were averaged to create an SSVEP. At least 500 segments were averaged for each SSVEP. Each SSVEP was then low-pass filtered at 30 Hz to remove high frequency and 50 Hz line noise (4th order Butterworth filter). An additional 10 ms were removed from each end of the segment to give one cycle of the SSVEP and to remove edge artefacts from the filter. For each SSVEP, the peak-to-peak amplitude was taken as the dependent variable. It is common in SSVEP experiments to perform a frequency transform (FFT) on a segment of the data to describe the amplitude of the evoked oscillation. However, here we chose not to do this for the main analysis: firstly because our particular artefact removal method works optimally for shorter segments in which an FFT would have very low resolution and secondly because the evoked oscillations are non-sinusoidal and would show higher harmonics which would be distributed across the FFT spectrum (in most cases a near 10 Hz oscillation was evoked from the flicker but in some participants the maximum was near 20 Hz, i.e. the first harmonic). Here, the SSVEP was treated more like a traditional event-related potential (ERP) and the peak-to-peak amplitude allowed the total size to be captured in a single number regardless of waveform shape. Example data are shown in Figure 3.

In addition to the main analysis, we determined the individual alpha frequency of each participant. To do this, the data from the inter-trial intervals in the baseline (no stimulation) condition were split into two-second segments centred on each ITI, segments containing eye blinks or movement artefacts were rejected as before, an FFT was performed on each, and the resulting spectra were averaged for each participant. The individual alpha frequency was defined as the peak of the averaged spectra between 8 and 14 Hz.

3 | RESULTS

3.1 | Behavioural data

For the analysis of the (non-parametric) behavioural data, Wilcoxon signed-rank tests were performed on the medians of the reported sensations of vection from after each 5 s trial. Effect sizes (r) for each test were calculated as $Z/\sqrt{}$(number of observations). Results showed significantly higher ratings of vection during optic flow compared with random dot movement in both baseline ($Z = -3.743$, $p < .001$, $r = -.599$) and 10 Hz tACS ($Z = -3.632$, $p < .001$, $r = -.574$), with no difference between baseline and tACS for either optic flow or random dots (the values were virtually identical). This means that, on average, participants reported feeling vection significantly more during the 5 s optic flow trials than in the control condition and that tACS did not affect this. Response to random dots was 'No vection' 81.7% and 82.3% of the time, respectively, for baseline and tACS conditions. In contrast, during optic flow

participants only reported 'No vection' 16.9% and 18.9% of the time and reported weak, moderate or strong vection for the majority (see Figure 4). Wilcoxon signed-rank tests showed no significance difference between vection sensations for 8.5 Hz and 9.9 Hz flicker in either the baseline ($Z = 1$, $p = .317$) or the tACS conditions ($Z = 1.414$, $p = .157$).

3.2 | EEG analysis

As the data were not normally distributed in some conditions, Wilcoxon signed-rank tests were used throughout.

3.3 | Lateralization during vection, experiment 1

To test whether lateralization changed with optic flow, the ratio of the amplitudes of the SSVEPs from P3 and P4 were calculated. Wilcoxon signed-rank tests were applied to the P3/P4 amplitude ratios (Figure 5, right panel), and Bonferroni corrections were applied to control for multiple
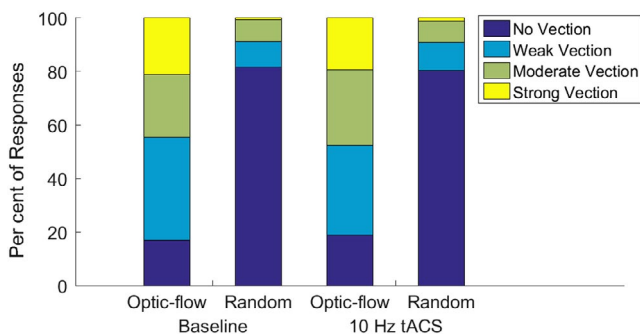
comparisons (adjusted alpha = 0.0125). Without stimulation, lateralization was significantly different between vection and random dot movement ($Z = -2.763$, $p = .006$, $r = -0.437$), being left lateralized during optic flow and right lateralized during random dot movement. For the 1 mA 10 Hz tACS condition, results show no significant difference during tACS ($Z = -1.755$, $p = .079$, $r = -.27$). Contrary to our hypothesis, tACS did not have effects on lateralization, that is there was no difference between optic-flow P3/P4 ratios with and without tACS ($Z = -0.709$, $p = .479$, $r = -.224$), and for the random dot condition, the ratios were almost identical ($Z < 0.001$, $p > .9$). To test for a relationship between vection strength and lateralization, a median split was performed on all participants' average reports of vection strength; a Wilcoxon signed-rank test showed no significant effect of P3/P4 ratio for either baseline condition ($Z = 0.97$, $p = .33$) or 10 Hz tACS ($Z = -0.66$, $p = .51$).

3.4 | Hz tACS increased SSVEP amplitude, experiment 1

To examine the effect of tACS on SSVEP amplitude at individual electrodes, Wilcoxon signed-rank tests were conducted comparing 10 Hz tACS to baseline (i.e. no tACS) for each optic flow condition and electrode. Bonferroni corrections were applied to control for multiple comparisons (adjusted alpha = 0.0125). A significant effect of tACS on amplitude was found in all conditions, with a higher amplitude being observed during tACS compared with baseline: P3 optic flow ($Z = -3.920$, $p < .001$, $r = -.62$), P3 random ($Z = -2.949$, $p = .003$, $r = -.47$), P4 optic flow ($Z = -3.733$, $p < .001$, $r = -.59$) and P4 random ($Z = -3.771$, $p < .001$, $r = -.60$). This shows that although 10 Hz tACS did not have any vection-specific effects, 10 Hz tACS did increase

FIGURE 4 Total percentage of all responses to the amount of vection participants felt after each 5 s trial from all 20 participants from experiment 1 [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 Mean peak-to-peak SSVEP amplitudes from electrodes P3 and P4 only (left) and mean P3/P4 ratios (right) for all 20 participants from experiment 1, for the baseline and 10 Hz 1 mA tACS conditions. Error bars indicate one standard error of the mean (*SEM*) [Colour figure can be viewed at wileyonlinelibrary.com]
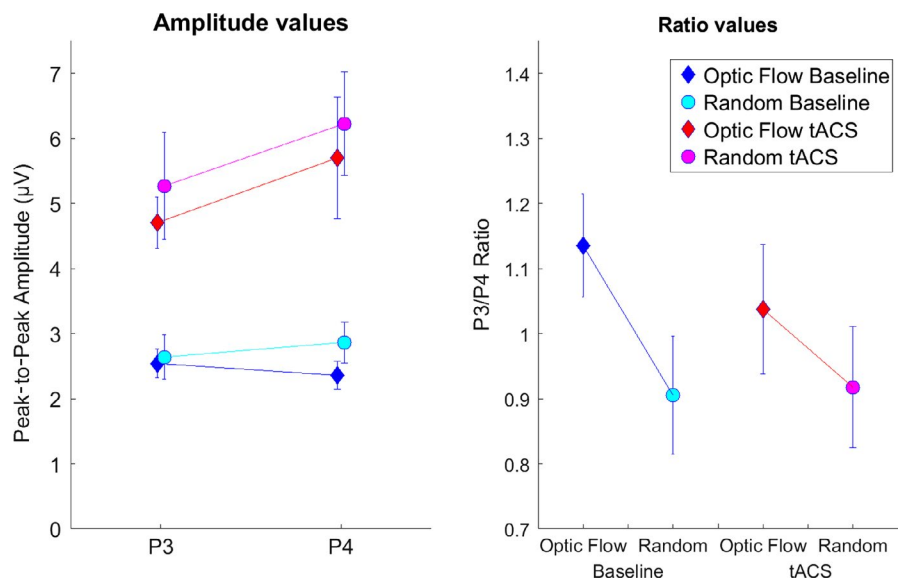
SSVEP amplitude across all conditions and both hemispheres (Figure 5, left panel).

Part of the second hypothesis (see Introduction) was that the tACS applied to O2 would increase SSVEP amplitude in the right hemisphere significantly more than the left hemisphere. Instead, we found that SSVEP amplitude was increased by a large amount in both hemispheres, which may be due to a number of reasons (see discussion). Although the P3/P4 lateralization in baseline and tACS for the random motion condition were very similar, indicating that the effect of right hemisphere tACS on lateralization was mainly stimuli specific to optic flow (Figure 5, right panel), the absence of any significant lateralization during tACS makes interpretation difficult. Accordingly, this prevents concluding that the tACS is selectively targeting one hemisphere or selectively disrupting lateralization. Further analysis of the data is therefore focused on the control conditions and demonstrating that the overall increase in SSVEP amplitude is not due to any residual artefact.

3.5 | Lateralization during vection is specific to SSVEP flicker frequency, experiment 2

Wilcoxon signed-rank tests were performed on the P3/P4 ratios of optic-flow and random dots movement for baseline and 10 Hz tACS for both 9.9 Hz flicker and 8.6 Hz flicker (Bonferroni adjusted $p = .0125$). Again, results show a significant difference between optic-flow and random dot movement in the 9.9 Hz flicker baseline condition ($Z = -2.599$, $p = .009$, $r = -.581$) replicating the first experiment (here with 10 rather than 20 participants). This significant difference for 9.9 Hz flicker was not present during frequency-matched tACS, again replicating the first experiment ($Z = -0.357$, $p = .721$, $r = -.079$). In addition, this experiment investigated the effect of different SSVEP flicker frequencies. P3/P4 ratios were not significantly different in the 8.6 Hz flicker with or without stimulation (baseline, $Z = -1.58$, $p = .114$, $r = -.353$: 10 Hz tACS, $Z = -1.274$, $p = .203$, $r = -.28$). This demonstrated that the lateralization effect found in both experiments in the 9.9 Hz flicker does not hold when the flicker is 8.6 Hz: optic-flow only affected lateralization with SSVEPs at near 10 Hz and not

when at a lower frequency. It is of note here that FFT spectra of the baseline ITI showed that 19 out of 20 participants across all experiments had an individual alpha frequency of 10 Hz or higher: and so this specificity of the lateralization effect at 9.9 Hz could be explained as an interaction of the SSVEP with the ongoing alpha-band oscillations.

3.6 | tACS frequency control

To confirm that only 10 Hz tACS, and not 8.3 or 12.5 Hz, was increasing the amplitude of the SSVEPs, the control conditions were compared with the active and baseline conditions. Here, we wanted to confirm that the SSVEP amplitudes in the control conditions were not only significantly different from the active condition (1 mA 10 Hz tACS) but also highly similar to the baseline. A standard null hypothesis test would not be appropriate as a p-value greater than 0.05 does not provide evidence for the null (Dienes, 2014); here, we report Bayes factors showing the relative probability of the data from the control condition coming from either the baseline or the active condition (the prior hypothesis). Bayes factors were calculated in MATLAB using a calculator by Dienes (2008); the suggested standard deviation transformation ($S^1 = S*(1 + 20/n^2)$) was applied to correct for the small sample size ($n = 10$) which may not be normally distributed. As the goal of these analyses is to demonstrate the likelihood of the null, the inverse Bayes factor is reported (BF10 = 1/BF01), for example a factor of 10 would indicate that the data in the control condition are 10 times more likely to come from the baseline distribution than the active condition. A factor of more than 3 is often considered moderate evidence, and a factor of more than 10 indicates strong evidence. Results are shown in Table 1. For both flanker frequency control conditions, the evidence was either moderately or strongly in favour of the null (Figure 6).

In addition to the tests on SSVEP amplitude, visual inspection of the SSVEP waveforms shows a very close match in both amplitude and waveform/phase for the baseline and flanker frequency conditions indicating that the tACS had no effect and the signal could be correctly recovered (see Figure 3 for example).

TABLE 1 Bayes factors showing the relative likelihood of the data from each control condition coming from the distribution of the baseline condition vs. the 1 mA 10 Hz condition. The conditions where the Bayes factor is less than 3 are in bold

Control condition	Optic-flow P3	Optic-flow P4	Random motion P3	Random motion P4
8.3 Hz tACS	25.53	13.95	12.5	9.16
12.5 Hz tACS	3.62	10.98	9.9	10.65
0.1 mA tACS	16.98	16.96	4.93	9.48
0.5 mA tACS	3.08	**2.61**	**0.26**	3.66

3.7 | tACS intensity control

To confirm that only 1 mA tACS, and not 0.1 or 0.5 mA tACS, was increasing the amplitude of the SSVEPs, Bayes factors were calculated as in the frequency controls (Table 1). The 0.1 mA control condition shows a strong likelihood of the null (Figure 7). Again, visual inspection of the SSVEP waveforms shows a very close match in both amplitude and waveform/phase between the baseline and 0.1 mA tACS. The 0.5 mA tACS seemed to have some effect at P3 (see discussion). A Bayes factor between 3 and 0.33 is considered inconclusive, indicating that there is insufficient evidence to determine an effect of 0.5 mA tACS during optic-flow. A Bayes factor of <0.33 can be considered moderate evidence of an effect, that is 0.5 mA at P3 during random motion (see discussion).

3.8 | Flicker frequency control, experiment 2

To confirm that tACS at 10 Hz did not significantly affect SSVEP amplitude from 8.6 Hz flicker, Bayes factors were calculated as in the main experiment. In this case, there was a separate baseline condition for each frequency; the alternative hypothesis (prior) was the difference between the 9.9 Hz flicker baseline and 9.9 Hz Flicker with 10 Hz tACS (which was significant), and the null hypothesis was the difference between 8.6 Hz flicker baseline and 8.6 Hz flicker with 10 Hz tACS. Results are strongly in favour of the null hypothesis for both P3 and P4 in both optic-flow (Bayes factors: 6.49 and 20.7) and random dot motion (Bayes factors: 12.37 and 5.14), i.e. no effect of 10 Hz tACS on 8.5 Hz SSVEPs (Figure 8).

FIGURE 6 Mean peak-to-peak SSVEP amplitudes for 10 subjects with frequency control conditions, for optic-flow condition (left) and random dot motion (right). Error bars show one SEM [Colour figure can be viewed at wileyonlinelibrary.com]
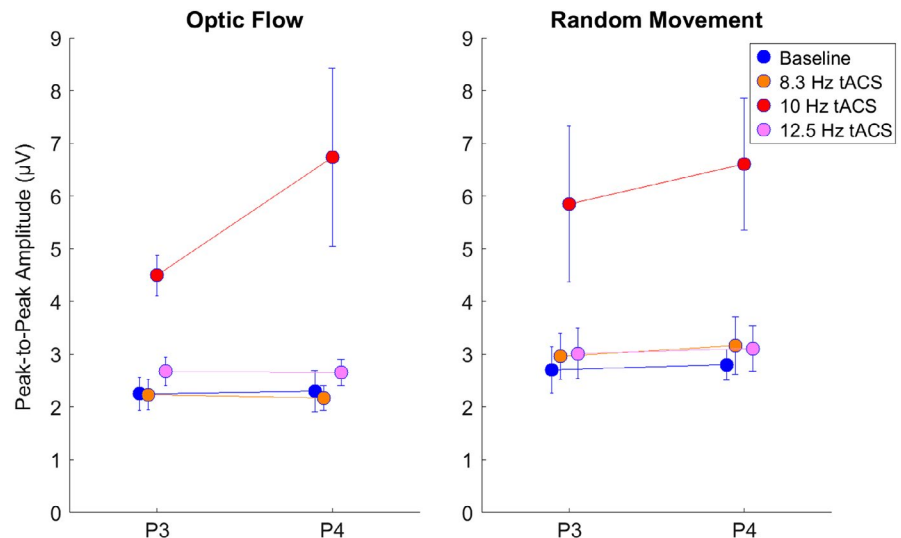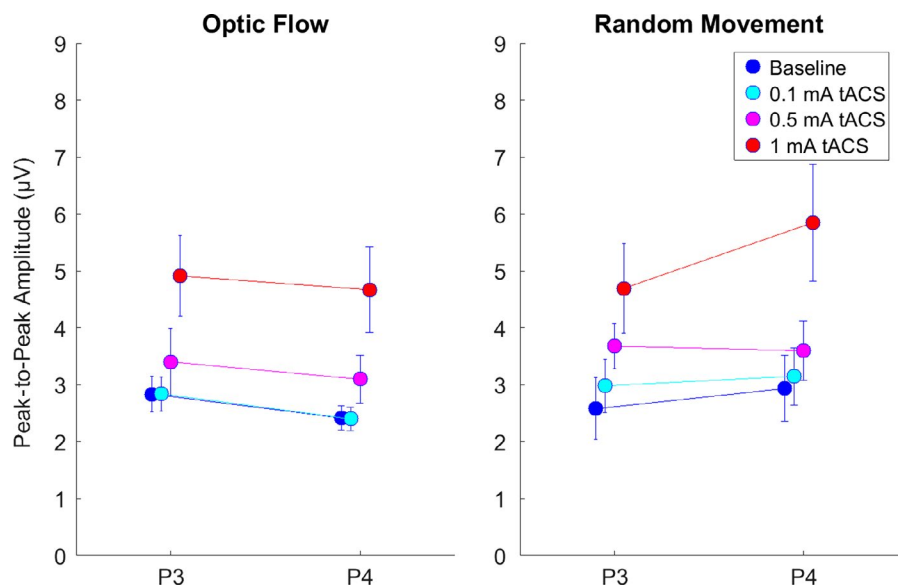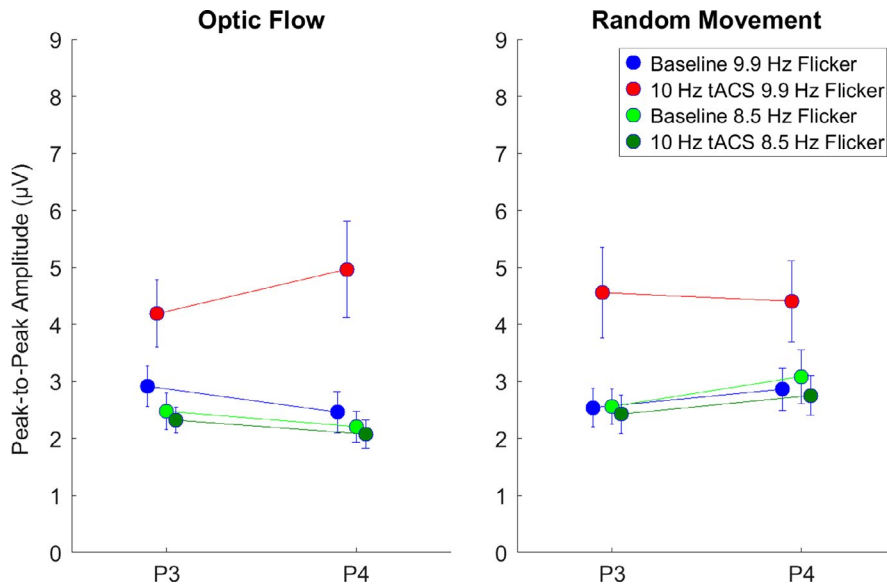

FIGURE 7 Mean peak-to-peak SSVEP amplitudes for 10 subjects with tACS intensity control conditions, for optic-flow condition (left) and random dot motion (right). Error bars show one *SEM* [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 8 Mean peak-to-peak SSVEP amplitudes for experiment 2 (10 participants) for optic-flow condition (left) and random dot motion (right). Error bars show one *SEM* [Colour figure can be viewed at wileyonlinelibrary.com]

3.9 | Permutation tests on individual subjects

An important problem for tACS, and brain stimulation generally, is that different individuals can respond to stimulation differently for any number of reasons (see discussion), and some individuals may not respond at all. In addition to the significant group-level effect, a significant effect at the individual subject level would be particularly useful as an indication of how well this method could be used to separate responders and non-responders to tACS.

An advantage of SSVEPs is the large number of trials that can be collected in a short amount of time. We took advantage of the large number of trials (>500) which are used to create each waveform to test for the significance of the increase in amplitude of SSVEPs at the individual subject level using permutation testing. Specifically, we looked for a significant increase in amplitude during tACS. For each subject, vection condition and electrode (P3 and P4), pairs of random SSVEPs were created by pooling trials from the baseline and tACS condition and randomly selecting half the trials for each. The difference in peak-to-peak amplitude between the two waveforms was taken as the output. This was repeated 1,000 times to create a normal distribution for the null hypothesis and compared with the true difference (baseline vs. tACS). *P*-values were calculated from the normalized distance of the actual value from the distribution of the random values following the procedure described by Cohen (2017).

Significance level was Bonferroni adjusted for 10 participants, two vection conditions, three stimulation conditions and 2 electrodes (0.05/(10*2*2*3) = 0.000417). Tables 2 and 3 show the number of participants for whom there was

TABLE 2 Results of randomized permutation tests for the frequency control conditions. Number of participants, out of 10, who showed a significant difference in SSVEP amplitude between baseline and tACS at the individual level (Bonferroni corrected). Bold indicates at least half the participants showed a significant effect

tACS Frequency	Optic-flow P3	Optic-flow P4	Random motion P3	Random motion P4
8.3 Hz	0/10	0/10	0/10	0/10
10 Hz	4/10	**5/10**	3/10	**5/10**
12.5 Hz	0/10	0/10	1/10	1/10

TABLE 3 Results of randomized permutation tests for intensity control conditions. Number of participants, out of 10, who showed a significant difference in SSVEP amplitude between baseline and tACS at the individual level (Bonferroni corrected). Bold indicates at least half the participants showed a significant effect

tACS Amplitude	Optic-flow P3	Optic-flow P4	Random motion P3	Random motion P4
0.1 mA	0/10	0/10	2/10	2/10
0.5 mA	2/10	2/10	3/10	3/10
1 mA	2/10	**5/10**	3/10	**5/10**

a significant difference between baseline and tACS for each control condition (10 subjects each). For electrode P4, there was a significant effect at the individual subject level for half of the participants, whereas in the 8.3 Hz, 12.5 Hz and 0.1 mA control conditions there is either no significant effect or only significant for one or two people (possibly due to order of conditions or after-effects of stimulation). In the 0.5 mA condition, two subjects reached significance during optic-flow and three during random dot motion.

3.10 | Individual alpha frequency

The FFT spectra from the inter-trial intervals showed a mean frequency of 10.4 Hz (max. 11.5 Hz min. 8.5 Hz) across all participants. It is of note that only one participant had an individual alpha frequency below 10 Hz, that is all others were between 10 and 11.5 Hz and therefore both above and quite close in frequency to the tACS and the visual flicker.

3.11 | Post-experiment questionnaire

The average response to the overall feeling of vection across the entire experiment was 66.5% for optic flow and 10.35% for random dot movement for experiment 1, and 55.7% and 18.5% for experiment 2. In answer to the question 'Did you ever feel dizzy or disorientated?': for experiment, 1, 8/20 responded 'yes' for the optic flow condition and 6/20 responded 'yes' for the random dot motion, and in experiment 2, 3/10 responded 'yes' for each condition (although not the same participants). In response to the question of whether or not they saw phosphenes during the tACS, only two participants from all 30 participants across all three experiments reported seeing phosphenes, and one of these reported that this was only at the beginning of the stimulation.

3.12 | tACS sensation

The median responses to the question of whether participants felt the tACS more or less than at the beginning of the experiment were calculated (0 = no sensation, 1 = less, 2 = same and 3 = more). For the tACS frequency and flicker frequency experiments, the median scores were zero for baseline and one for all tACS conditions. For the tACS intensity experiment, the median scores were one for 1 mA tACS and zero for all other conditions. Therefore, most participants felt the stimulation less as the experiment progressed. Wilcoxon signed-rank tests showed no significant differences between any conditions ($p > .1$ in all cases). These values were highly variable with some participants feeling nothing in both experiments (11 out of 20 participants had a median response of zero during stimulation), which explains the lack of a significant difference between the sensation in the baseline and 1 mA tACS conditions at the group level. Importantly, the

sensations were indistinguishable between the various frequencies of tACS so the significant effect of 10 Hz stimulation cannot be due to sensation. When participants were grouped into those who did versus did not report feeling the tACS, these groups did not differ in how much 10 Hz tACS increased SSVEP versus baseline (Mann–Whitney U tests; all p's > .43), indicating that any relationship between tACS sensation and the increase in SSVEP amplitude is unlikely.

4 | DISCUSSION

This study shows that optic flow (which induced the perception of self-motion, i.e. vection) evokes lateralized responses compared with random dot motion when flickering in the alpha range and that SSVEPs can be enhanced with frequency-matched tACS.

4.1 | Optic flow evokes lateralized responses

For most (right-handed) individuals, the SSVEPs (in the no stimulation baseline condition) shifted to being smaller in the right hemisphere and/or larger in the left hemisphere during optic flow relative to random dot movement. Inspection of the SSVEP amplitudes indicated that this effect was largely driven by differences in the right hemisphere. This main finding provides additional evidence for the lateralization of visual–vestibular function. The two conditions were matched for total luminance and were on average symmetrical in the vertical midline so the lateralization in the baseline condition cannot be explained by low-level stimulus properties. This supports a role for alpha lateralization in higher vestibular cognition, that is the processing of optic flow that is consistent with self-motion.

A possible interpretation, which cannot be ruled out in the current study, is that the lateralization is the result of the globally coherent motion in the optic flow condition, independently of the sensation of vection. The primary goal of the current stimulus design was to find a reliable neural correlate of optic flow which is able to induce vection (and to test if this measure can be manipulated with tACS), to serve as a frequency-specific metric for future investigations into visual–vestibular integration. Designing a visual stimulus that involves globally coherent radial motion but does induce vection, or vice versa, is challenging because globally coherent motion is a fundamental property of optic-flow that causes vection; we have recently reported some findings developing stimuli which are a hybrid between optic-flow and random movement (Dowsett, McAssey, Dieterich, & Taylor, 2017).

The lateralization effect could be seen in the baseline condition with 9.9 Hz flicker in experiment 2, but not in the 8.6 Hz flicker conditions (either during baseline or 10 Hz tACS). FFT spectra of the baseline data from the inter-trial

intervals showed that almost all participants had an individual alpha frequency of 10 Hz or higher. This implies that the P3/P4 lateralization effect may be exclusive to flicker frequencies close to the natural alpha frequency. However, this should be interpreted with caution as the difference may be due to the visual properties of the lower flicker frequency. Future research will test a greater range of flicker frequencies, including some above the alpha band, to determine whether this effect is truly an interaction with individual alpha frequency.

4.2 | tACS significantly enhances SSVEP amplitude

Stimulation was applied to electrode position O2 with the intention of selectively modulating right hemisphere. However, SSVEP amplitude was significantly enhanced in both hemispheres. Although the overall effect of frequency-matched tACS was to nullify the lateralization effect, the lack of any significant difference between the lateralization of the optic flow SSVEPs in the baseline and the 10 Hz tACS conditions precludes the comparative claim that the effect of tACS on lateralization was state specific. There are a number or possible explanations for the effect of tACS at O2 occurring over both hemispheres: firstly, the current could have spread across the midline; the relatively large electrodes used do not deliver a focal current; and O2 is only about 3 cm from the midline. Another explanation is that the enhancement of the SSVEPs in the right hemisphere indirectly entrained the oscillation in the left hemisphere. Distinguishing between these possible mechanisms requires additional experiments with a more focal montage and various control sites. Given the results of the first experiment, we chose to focus the analysis on the amplification of SSVEPs and demonstrating that this is not due to residual artefact. However, the lateralization ratio in the random condition was very similar between baseline and 1 mA 10 Hz tACS (0.90 and 0.91 respectively) which indicates that the effect on lateralization may be specific to optic flow to some extent (Figure 5, right).

Transcranial alternating current stimulation consistently increased the amplitude of SSVEPs only when the frequency was closely matched, and the amplitude was sufficiently high. All control conditions across all three experiments (except 0.5 mA tACS, see below) showed no effect of stimulation in the peak-to-peak amplitude of the SSVEPs. Taken together, this is good evidence that the most prominent effects of tACS occurred when the frequency closely matched the ongoing neural activity and was of sufficient amplitude. Progressively weaker alternating currents have been shown to be able to entrain neural activity as the stimulating frequency approaches the frequency of the neuronal oscillation, a relationship known as an Arnold Tongue: the maximal effect is predicted to be when the frequency of the neuronal

oscillation and the stimulation are closely matched (Fröhlich, 2014; Thut et al., 2017). A number of tACS experiments have attempted to optimize the efficacy of stimulation by matching the frequency of the stimulation to individual alpha frequency (Kasten & Herrmann, 2017; Neuling, Rach, & Herrmann, 2013; Zaehle, Rach, & Herrmann, 2010). However, naturally occurring oscillations are not at a stable, precise frequency and can shift in phase and frequency over time and depending on task. Combining SSVEPs and tACS can provide a solution as the frequency of the induced neuronal oscillation can be precisely controlled because it will always follow the driving flicker of the visual stimulus. This could increase the efficacy of tACS, although strictly speaking there is no phase or frequency shift of the SSVEP as it is frequency locked to the visual flicker. Rather, what we observed here can be described as 'constructive interference' between the neural oscillation and the stimulation. This effect is present when the tACS and neural oscillation are close but not exactly matched (9.9 Hz flicker, 10 Hz tACS), demonstrating that neural and external oscillators do not have to be exactly the same frequency to show significant enhancement. This could help bypass some of the technical difficulties involved in stimulating and recording at exactly matched frequencies.

Transcranial alternating current stimulation did not have clear effects on lateralization (although some evidence was present in the absence of lateralization during tACS, this did not differ statistically from the no stimulation condition). Null effects from tACS are hard to interpret, due to the factors to which tCS experiments in general are sensitive (Parkin, Ekhtiari, & Walsh, 2015) and so this does not indicate that tACS cannot in principle affect lateralization but rather leaves it an open question for the future.

4.3 | Artefact removal

The artefact removal method used here has a number of advantages over other methods. The template subtraction algorithm is no more likely to leave a residual artefact in any one of the tACS frequency conditions; this is because the SSVEP is treated like a traditional ERP, and only a short segment of data, approximately the length of one cycle of the stimulation, has the artefact removed at any one time. The 0.1 mA control condition showed no effect, which excludes the possibility that removing an artefact at 10 Hz leaves a residual artefact, and the flicker frequency control (10 Hz stimulation with 8.6 Hz flicker) showed no effect on the amplitudes of the SSVEPs, which excludes the possibility that creating a template from 10 Hz 1 mA stimulation leaves a residual artefact or somehow corrupts the data.

An advantage of sawtooth waves (and square waves) is that template subtraction is much less susceptible to residual artefacts resulting from any differences in phase between the
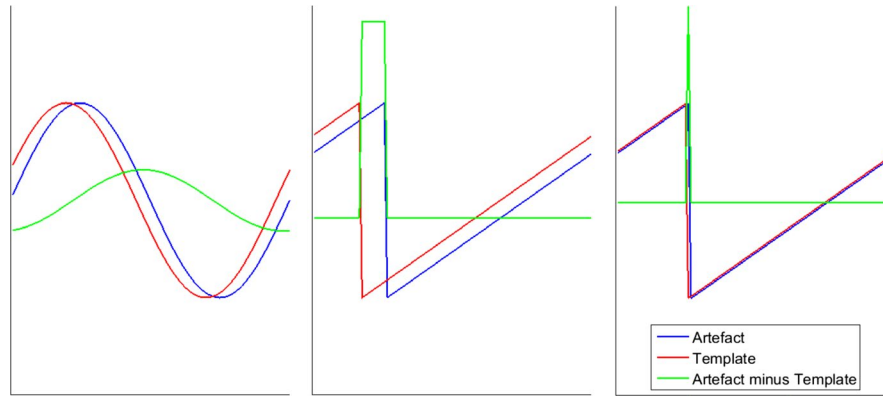
FIGURE 9 Simulated data to illustrate the properties of subtracting a template from an artefact if the phase is slightly different. Subtracting a sine wave from a sine wave will result in a small phase shifted sine wave, which could be mistaken for neural activity. Subtracting a sawtooth wave from a sawtooth wave will result in a square wave pulse as large as the original signal, even if the phase difference is one data point. This makes phase differences between artefact and template easy to observe and avoid [Colour figure can be viewed at wileyonlinelibrary.com]

artefact and the template. Any slight differences in the phase of the template and artefact will result in a large residual artefact with the same amplitude as the artefact itself, specifically a square wave pulse. Any such segment will not be selected by the template construction algorithm. Figure 9 shows simulated data to illustrate the properties of subtracting a template from an artefact if the phase is slightly different. In the case of sine waves, the result is always a sine wave, and as the phase difference decreases, the amplitude of the resulting sine wave is reduced, but is never zero unless the phase difference is exactly zero (Figure 9 left panel). This is a significant problem for tACS artefact removal using template subtraction because small residual sine waves can easily be mistaken for entrained brain activity. For sawtooth waves, the result is always a large rectangular pulse which is as large as the artefact itself, clearly visible and cannot be mistaken for neural activity (Figure 9, centre). This is true even if there is a difference in phase of only one data point (Figure 9, right panel). Therefore, as no such residual artefacts are present, we can be sure the phase of the template is correct in all cases.

The phase of the tACS was drifting relative to the SSVEP in all conditions (because the flicker frequency was not exactly 10 Hz). Inspection of the raw segments revealed that all relative phases are equally present in all conditions over the course of the experiment: all segments were split into 8 phase bins of tACS phase relative to flicker, and each condition contained at least 30 segments in each phase bin. Any small residual artefact that may have been left in the raw segments would not be phase locked to the flicker and would be greatly reduced in the process of averaging. As such, we can be confident that the effect is a genuine manipulation of neural activity.

4.4 | Peripheral nerve stimulation

An important concern for tACS studies is the possibility of the effects being due to peripheral nerve stimulation: either sub-threshold phosphenes due to current reaching the retina (Kar & Krekelberg, 2012) or stimulation of nerves in the scalp (Asamoah et al., 2019). In our experimental design, the tACS is running continuously, and the visual flicker was present for 5-second blocks, with a five-second inter-trial interval (ITI). The template of the tACS artefact was created from segments from the ITI and subtracted from the flicker period. Any tactile-evoked potential or peripheral nerve/retinal stimulation from the tACS would be identical in the ITI and the trial itself and would be subtracted along with the artefact. This rules out any possibility of a linear summation of visual- and tactile-evoked potentials being responsible for the main effect reported here. All relative phases of tACS and flicker were present in all conditions; during the frequency control conditions, the same current would be reaching the retina in the same distribution of phases. The most likely explanation for these findings is a direct effect of the electrical field on the cortical oscillation, rather than an indirect combination of sensory modalities, although future work should investigate whether it is possible to completely rule out that retinal/tactile-evoked potentials can entrain SSVEPs in a non-linear way. Additionally, 11 out of 20 participants did not feel any sensation from tACS, and those that did feel something from tACS found the different frequencies indistinguishable in terms of intensity, in that they did not notice the sensation changing over the course of the experiment. Although participants were not specifically asked whether they could distinguish the different frequencies, piloting indicated that participants were not aware of a difference between closely matched frequencies.

4.5 | Effect of 0.5 mA tACS

An additional finding of interest was an effect of 10 Hz tACS at 0.5 mA (1 mA peak-to-peak): the amplitude of SSVEPs was enhanced, although not consistently across participants.

We chose 1 mA (2 mA peak to peak) for the main stimulation condition because this intensity has shown effects in previous studies and stimulating at lower intensities was less likely to show an effect. However, the peak-to-peak amplitudes of the SSVEPs were clearly enhanced in some cases by the 0.5 mA tACS. The wide spread of SSVEP amplitudes during 0.5 mA stimulation across participants (i.e. a high standard deviation) might indicate responders and non-responders; this intensity may have been above the threshold required to affect neural oscillations for some participants and not for others. This is supported by the permutation tests on individual participants indicating some participants were responders and others either were non-responders or showed a weaker effect which would require more trials to be seen at the individual subject level. Another possibility is that the 0.5 mA tACS had a different effect from the 1 mA tACS due to non-linear effects of stimulation. Moliadze and co-workers reported that high-frequency tACS over the motor cortex led to increased cortical excitability with 1 mA, inhibition of cortical excitability at 0.4 mA and no effect with the intermediate 0.6 and 0.8 mA (Moliadze, Atalay, Antal, & Paulus, 2012). It is possible that such effects could also occur in the current paradigm.

4.6 | Frequency-specific SSVEP lateralization

The issue of whether SSVEPs in the alpha range are the result of entrained endogenous oscillations, or the superposition of event-related responses, is a topic of active debate (see Notbohm, Kurths, & Herrmann, 2016; for evidence supporting the entrainment hypothesis). The focus of this study was SSVEPs in the alpha range and not endogenous alpha oscillations, as SSVEPs have the advantage of a higher signal-to-noise ratio, making them well suited to clinical diagnostics where time is a limiting factor or to more naturalistic settings where movement artefacts are more common. Additionally, SSVEPs maximize the possibility of an interaction with tACS because the frequency can be precisely controlled. The frequency-specific SSVEP responses to optic flow and random movement could imply an entrainment of endogenous oscillations at these frequencies or a frequency-specific response of the cortex independent of pre-existing oscillations. Distinguishing between these interpretations is beyond the scope of this study, but SSVEPs are a useful research tool regardless of the specific mechanism.

4.7 | Effects at the individual subject level

The permutation tests on individual participants show that the effect of tACS on SSVEP amplitude is large enough to be seen at the individual level in half of the participants. The goal of these permutation tests was to demonstrate that the enhancement of SSVEP amplitude is large enough that this

method can potentially be used to separate responders from non-responders, in addition to the overall group-level effect. There are many reasons why some participants might respond to transcranial stimulation and others might not such as variations in skull thickness, thickness of cerebrospinal fluid, skin conductivity etc. (Laakso, Tanaka, Koyama, De Santis, & Hirata, 2015). However, an individual subject not reaching significance does not necessarily imply there is no effect; it could be the case that the number of trials was not enough to reach significance at the individual level for these subjects (for example due to high variability). This is supported by the fact that the direction of the effect (SSVEPs being larger during 10 Hz stimulation than baseline) was the same for almost all participants, hence the highly significant effect at the group level. This gives an indication of the number of trials needed to demonstrate an effect at the individual subject level with this set-up (i.e. more than 500, approximately 50 s of flicker at 10 Hz). More subjects reached significance at the individual level at electrode P4 than P3, implying that for some participants the effect was hemisphere specific to some degree.

The baseline SSVEPs did not show any consistent waveform or phase across participants. Different effects of any one montage across participants might be expected due to individual differences in cortical folding. This highlights the need for individualized stimulation parameters in future experiments. This experiment was not designed to investigate phase-specific effects in more detail as the 9.9 Hz flicker and 10 Hz tACS drifted in and out of phase at random.

4.8 | Limitations

This study used a comparatively small number of EEG electrodes to be optimally compatible with tACS, and this prevents whole-head topography mapping. Vection sensations were reported using a 4-point scale to confirm that participants were feeling vection: finer scales could provide the higher resolution necessary to investigate whether or not the lateralization effect correlates with the strength of vection. Participants only reported vection at the end of each 5-s trial, to prevent any neural activity related to response execution from confounding the SSVEPs. Here, we do not dissociate between whether this lateralization was caused by the optic flow or by the vection sensation it triggered. Behavioural data affirmed that the optic flow stimulus reliably induced vection (and in some cases even motion sickness). The primary goal of the vection sensation reports was to confirm that participants were feeling vection; a subsidiary hypothesis was that tACS would modulate this sensation, although we did not find evidence of this. This may be due to the limited sensitivity of the 4-point scale or the inter-subject variability in tACS effects: finer psychophysical measures could provide the higher resolution necessary to investigate whether or not the tACS effect correlates with the strength of vection.

Future studies, using the method described here, can optimize stimulation parameters and/or separate responders and non-responders (to vection and/or tACS), to maximize the likelihood of a behavioural effect of tACS. In our set-up, vection was elicited with relatively short stimulus duration of 5 s, whilst many previous experiments have employed longer durations e.g. 10 s and have found that vection becomes stronger with exposure duration (Palmisano & Riecke, 2018; Seno et al., 2018). The short vection onset latency may be due to the particular stimulus motion characteristics or the fact that participants were standing. A further possibility is that feelings of vection were affected by the visual flicker of the stimuli, which was used in our design in order to generate SSVEPs, as recent work has found that vection can be induced more rapidly using a coherent change in stimulus colour (Nakamura, Seno, Ito, & Sunaga, 2010).

5 | CONCLUSION

Firstly, a shift in lateralization of cortical responses to vection induced by optic flow could be observed in SSVEPs in the alpha range of right-handers. This is in line with current knowledge on the lateralization of vestibular function in the cortex and the role of alpha oscillations in multisensory integration and is a promising metric for future investigations into visual–vestibular integration.

Secondly, frequency-matched tACS was found to be a promising method for manipulating SSVEPs. Frequency and amplitude control conditions demonstrated that the effect of the tACS was only seen when the frequency of stimulation closely matched the flicker frequency, and the current intensity was sufficiently high. As this was a clear effect, visible at the individual subject level, it is a promising protocol for administering tACS in future studies.

DECLARATION OF INTEREST

CSH holds a patent on brain stimulation. All other authors declare no competing interests.

AUTHOR CONTRIBUTIONS

JD contributed to all aspects of the paper. CSH contributed to the design of the artefact removal procedure and edited the manuscript. MD contributed to the design of the experiment and edited the manuscript. PCJT contributed to the design of the experiment, artefact removal, data analysis and drafting and editing of the manuscript.

DATA AVAILABILITY

The authors are unable to make the participants' data publicly available due to the constraints of the ethical approval for this project. Example code is available on request.

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