A high-density EEG study of differences between three speeds of ecological forward motion in adult participants

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Abstract

A high-density EEG study was conducted to investigate evoked and oscillatory activity in response to three different stimulus speeds of simulated forward motion in adult participants. Participants were shown an optic flow stimulus consisting of a virtual road with moving poles at either side of it simulating forward motion at three different speeds (low, medium, and high) with a static control condition between each motion condition. The aim was to analyse the N2 component of visual motion and the evoked oscillatory activity in occipital and parietal areas.

A significant difference in N2 latencies and peak amplitudes between the three stimulus speeds were found in parietal channels P3 and P4. The peak latency significantly increased as the simulated speeds increased, while the peak amplitudes decreased at increasing speeds. The latency differences were thought to indicate that the low simulated speed was easier to process than the faster medium and high simulated speeds, while the change in peak amplitude seemed to be the result of a greater number of neurons being attuned to the lower as opposed to the higher stimulus speeds.

Theta-band synchronizations and alpha-band de-synchronizations in the three different speeds were observed, but no significant differences between the speeds were found. The static condition, in contrast, showed theta-band de-synchronizations and alpha-band synchronizations. Significant differences between the alpha de-synchronizations in the three different speeds and the alpha synchronizations in the static condition were found in the parietal midline source, while no significant differences were found between conditions in the theta oscillations. It was suggested that the alpha de-synchronizations reflect an activated state, possibly related to the visual processing of the three speeds, whereas the alpha synchronizations in response to the static condition reflect a deactivated resting period.

1.0 Introduction

Gibson (1966) argued that the information contained in the optic flow field is sufficient for manoeuvring in the environment, and several studies (Warren, Kay, Zosh, Duchon & Sahuc, 2001; Bruggeman, Zosh & Warren, 2007) have shown that optic flow information, indeed, gives vital clues about direction and heading.

Over the last few decades numerous studies on both optic flow and visual motion in general have gathered an immense amount of information on how our brains process this kind of information, and much is known about how human, and mammalian, brains deal with incoming visual information. However, still some questions remain regarding how naturalistic stimuli are processed. We constantly move around in an environment that changes according to our movements, and the optic flow field provides detailed information about our position in the environment and where we are heading (Bruggeman, Zosh & Warren, 2007; Bruggeman & Warren, 2010). When we increase our velocity the environment might be static, but not our position relative to it. How, then, does the brain process these changes in the flow field regarding our (perceived) velocity?

Optic flow is the sum of all the information contained in the visual array, resulting from the information contained in invariants in the environment created by motion. Invariants are unchanging physical properties in the environment. When light strikes objects and organisms, it is reflected and picked up by the eyes. The information is in the invariants, and the visual array is the sum of all the invariants (Gibson, 1966). One important aspect of optic flow is the static focus of expansion (FoE) (Warren et al., 2001), which shows heading, so that if the FoE moves then direction is seen to change. So moving objects would lack a FoE and only need motion in one of its two dimensions. It is therefore likely that the visual areas in the brain would differentiate between these types of motion. So the functional relevance of optic flow stimuli becomes apparent as it is an indicator of our motion through a three dimensional world. Optic flow-fields contain perspective, so the observer has information about the relative movements of objects in relation to the observer, so simulation of optic flow represents real-world motion.

Motion processing has been found to occur predominantly in the V5/MT area of the human brain. This has been shown in a number of different studies on motion perception (Basso et al., 2012; Holliday & Meese, 2008; Hayashi, Sugita, Nishida, & Kawano, 2010, Zeki, Watson, Lueck et al., 1991). In the primary visual cortex, visual information is carried down three different pathways where the magno-cellular M-pathway is mainly responsible for motion information and sends information to layer 4Cα in V1, through layer 4B, V3 and terminating in the extra-striate middle temporal (V5/MT) area and medial superior temporal (MST) area, also called the dorsal stream (Bear, Connors & Paradiso, 2007; Heinrich, 2007). It has also been shown, in both human and animal studies, that area 7a, the right latero-posterior precuneus (superior parietal lobe) and the motor cortex, above V5/MT and MST, are involved in the processing of motion, including optic flow, information (Phinney & Siegel, 2000; Merchant, Battaglia-Mayer & Georgopoulos, 2001, Merchant, 2004; Liu & Newsome, 2003).

The parvo-cellular pathway sends information, predominantly colour information, to layer 4Cβ in V1 and down the so called ventral stream (Bear, Connors & Paradiso, 2007), and will not be the focus in this paper. However, Gegenfurter and Hawken (1996) have argued that the M-pathway is not colour blind and the P-pathway is not motion blind. Evidence from primate studies suggests that the middle layers of the six pairs of the konio-cellular pathway relay information from short wavelength (blue) cones to V1, the two dorsal layers send information about low-acuity visual information to V1, while the ventral layers are involved in the function of the superior colliculus (Hendry & Reid, 2000).

Electrophysiological research on visual motion has identified an N2 or N200 component as the main component associated with motion stimuli in motion-onset experiments. Motion visually evoked potentials (M-VEPs) are usually elicited by presenting intermittent moving and stationary stimuli, which produce motion-onset potentials (Heinrich, 2007). The N2 component is prevalent in occipital and occipito-temporal sites (Probst, Plendl, Paulus, Wist & Scherg, 1993; van der Meer et al., 2008, Morrone et al., 2000), and typically has a latency of 130-250 ms (Kuba & Kubová, 1992; van der Meer et al., 2008). The component consists of an earlier positivity, P1 at around 130-150 ms, which is most likely pattern-dependent (Kuba & Kubová, 1992; Hoffmann, Dorn & Bach, 1999), while the N2 component reflects the motion component in the stimulus (Kuba & Kubová, 1992). The N2 latency and peak amplitude vary based on the velocity, direction, luminance, contrast, eccentricity of, and adaptation to, the stimulus (Heinrich, 2007; Müller & Göpfert, 1988; Schlykowa, van Dijk & Ehrenstein, 1993; Bach & Ullrich, 1993).

Several optic flow studies have been conducted to investigate the neurological basis for visual motion and to study the brain structures involved in this process, and the V5/MT and MST areas have been identified as being mainly responsible for processing optic flow (Duffy & Wurtz, 1997; Duffy, 1998; Morrone et al., 2000, Holliday & Meese, 2005, 2008), even though also higher areas receive and process information about optic flow. A large number of neurons in rhesus monkey MST area are also sensitive to a speed gradient stimulus, where the speed is slower in the centre of the stimulus, and increases towards the periphery (Duffy & Wurtz, 1997). Duffy and Wurtz (1997) found a difference between non-gradient and gradient stimuli as well, showing that the MST area is specialized for processing optic flow patterns. This was also seen in an animal (macaque monkey) study by Liu and Newsome (2005), where, by looking at single cells and multi-unit clusters, they found activation in the MT area. There seems to be sensitivity to ecological stimuli in the MT/V5 and MST areas, although these areas also respond to translational and non-gradient visual motion stimuli. Van der Meer et al. (2008) conducted a high-density EEG study to investigate infants' and adults' brain responses to optic flow comparing structured forward optic flow to random visual motion. They found latency differences between adults and infants, where infants seemed to process information slower, as shown by higher N2 latencies. Both groups had lower N2 latencies for structured motion compared to random motion, and this was interpreted to be a result of more coherence in, or reflect the higher importance of, structured motion.

The amplitude and latency of the N2 component have also been linked to the velocity of the stimulus, and a decrease in latency and an increase in amplitude for increasing visual motion velocity is the most common finding (Heinrich, 2007). Maruyama, Kaneoke, Watanabe and Kakigi (2002) found this using a random dot kinematograph (RDK) and different stimuli speeds in a MEG study. Another MEG study, conducted by Kawakami et al. (2002) using a higher range of speeds reported the same results, but when stimulus speed increased to above 100 °/s the latency increased. Stimuli in these two studies are in some ways fundamentally different from optic flow, as they are representations of object-motion. Object-motion stimuli are often moving dots as in the two above studies or translational drifting checkerboard (or sine wave) gratings (as in Kuba & Kubová, 1992), and are unrelated to ego-motion.

Lately, there has been more and more focus on analysing oscillatory EEG activity. Responses that are not phase-locked (evoked) to the event are cancelled out in the averaging process (Pfurtscheller & Lopes Da Silva, 1999; Bastiaansen, Mazaheri & Jensen, 2012). These non-phase-locked changes in oscillatory activity allow us to analyse activity that might be unseen if we only look at the phase-locked activity. (De)-synchronizations are related to couplings and un-couplings of neuronal networks. One of the advantages of repeated firing in neurons is that they are more likely to co-activate other neurons and engage in oscillatory activity, and these (de)synchronous activities reflect changes within neuronal networks. There is a continuous oscillatory activity, and responses to this activity, e.g. experimental effects, are modulations to this on-going activity (Bastiaansen et al., 2012). The speeds at which neurons, and neuronal networks, fire, allow them to participate in different processes. This means that one neuronal network can process several events, and a single neuron can therefore contribute to different networks (Bastiaansen et al., 2012).

To be able to analyse these time-locked, but non-phase-locked (induced) changes in the EEG data, a time-frequency analysis is conducted. The changes in the time-spectrum evolution (TSE) are called event-related synchronizations (ERS) or de-synchronizations (ERD) (Pfurtscheller & Lopes Da Silva, 1999).

In connection with visual stimulation, alpha-band oscillations are linked to either an attentive or an idling state. Synchronizations often reflect the idling state, while a following or earlier de-synchronization reflects an activation period or an attentive state (Pfurtscheller, Neuper & Mohl, 1994; Klimesch, 1999).

The activated state can be a preparation for or the execution of a motor behaviour (Pfurtscheller & Berghold, 1989). Two separate alpha ERDs are often found: one lower alpha situated in occipital areas, and one higher alpha situated over parietal areas. The former has been linked to processing of visual stimuli, while the latter is thought to be involved in cognitive processes and attention (Pfurtscheller, Neuper & Mohl, 1994).

The current study investigated how the brain interprets speed differences in visual motion. The goal was to determine, using high-density EEG, how the occipital and parietal areas respond to three different speeds. No EEG research, to our knowledge, has investigated the response to different speeds in an optic flow paradigm. Our goal was to study how the brain processes different speeds of forward motion. We therefore set up an experiment similar to previous optic flow studies (van der Meer et al., 2008), creating a realistic scene which investigated perception of speed changes in ego-motion. This was different from several previous EEG studies on velocity, which have tested object-motion.

A novel motion stimulus was used, where the participants looked at approaching poles on each side of the visual field, where the poles were presented at three different speeds simulating self-motion down a road. It was expected that a difference between the speeds in the recorded VEPs would be observed, but how the latencies and amplitudes would be affected by the different speeds was unknown. Latency and amplitude findings obtained from previous studies that used checkerboard gratings and random dot cinematographs simulating object-motion were compared to those in the present study, where more ecologically valid stimuli simulating ego-motion were used.

Thus, the aim of the current study was to record electrical brain responses to visual motion simulating forward ego-motion using high-density EEG and analyse visual components in the corresponding VEPs. Whether, and, if so, how the speed differences affected the induced non-phase-locked changes in the time-speed domain was investigated.

By understanding how the brain reacts to an ecologically plausible stimulus moving at different speeds, we might come closer to understanding how real world events, and differences between these, are processed by the motion sensitive areas of the brain.

2.0 Method

2.1 Participants

Participants were recruited from the Dragvoll campus, NTNU. Twelve participants were tested (7 males), between 18 and 33 years of age (Mean=25 years, SD=3.8). All participants were right-handed, and had normal or corrected-to-normal eyesight (one participant wore glasses during the experiment). Two male participants could not be included in the analyses due to excessive noise in the data, resulting in ten participants (five males) whose data were analysed. Before signing a consent form, participants were given an information letter explaining the purpose of the study and they were informed that they could at any time, without consequence, abort the experiment. This study has been approved by the Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences.

2.2 Stimuli

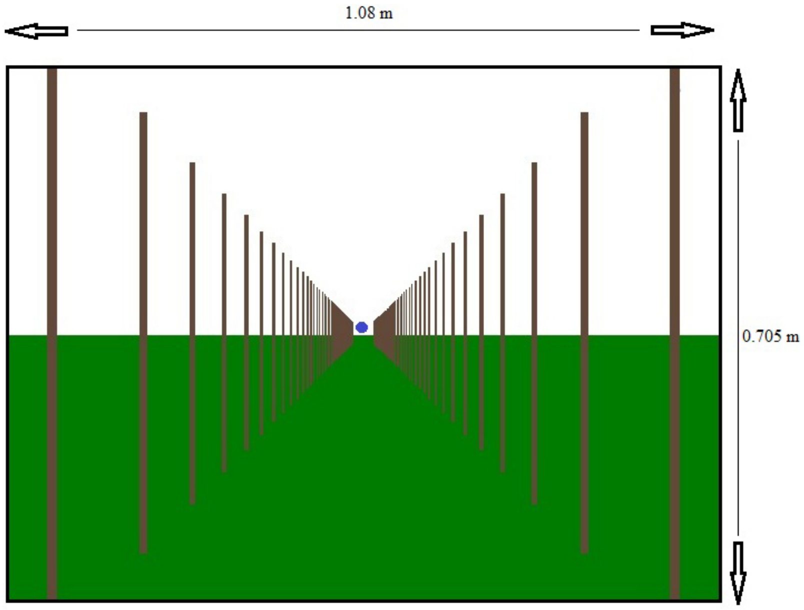

Figure 1 *Screen shot of medium speed optic flow stimulus simulating forward ego-motion. Blue dot in the centre of the screen indicates where participants were instructed to look, but was not present during the experiment.*

The stimuli were generated by E-Prime software (Psychological Software Tools, Inc.) and mirror-projected onto a screen (1.08 m x 0.705 m) by an ASK M2 projector with a refresh rate of 60 Hz. The screen had a resolution of 593 pixels/meter. The participants were seated approximately 75 cm from the screen so that the screen subtended an angle of 71.5° by 50.4°.

Vehicle driving at three different speeds was simulated by showing forward motion on the screen. The three different speeds were set to 24.8 km/h, 49.7 km/h, and 74.5 km/h, and are referred to as low, medium and fast speed, respectively. Participants were shown several poles, which started from the centre of the screen and travelled outwards, leaving the screen at each side, which simulated forward motion (see Figure 1). The visual angles, defined by the first (road end) and last (road start) position of the poles, resulted in a road length of 30 metres.

So as to prevent motion adaptation, a static control condition was shown after every forward motion condition. This inter-stimulus interval (ISI) was created by showing a static stimulus consisting of the same number of poles as in the preceding trial. This was done to avoid any difference in luminance between the forward motion conditions and the static condition.

The forward motion trials lasted 1000 ms each, while the static control trials lasted 3000 ms, giving a duty-cycle of 3:1. There were 75 trials for each of the three forward motion conditions, and 225 trials for the control condition, so the experiment took a total of 15 minutes.

All participants were monitored via two digital videos cameras, and five participants had their gaze monitored by a Tobii X50 camera, but gaze data were not used for further analysis. It was confirmed that participants were able to hold their gaze firmly in the centre of the screen and very seldom moved their eyes.

This study used chromatic stimuli with a green ground and brown poles on a white background (top half of the screen). The speed of the stimuli had to be kept below approximately 100 km/h because at these speeds participants in a pilot study reported a reversal and momentary standstill of the stimulus, a phenomenon known to be a result of spatial under-sampling (Wang, Thibos & Bradley, 1996). None of the participants reported this effect in the current study, indicating that we successfully managed to avoid it.

2.3 Apparatus

Electroencephalogram (EEG) activity was recorded using a high-density Geodesic Sensor Net 200 (GSN) (Tucker, 1993). The net consisted of 256 Ag/AgCl sponge sensors, and three different sized nets (small, medium, and large) were used depending on the participant's head size. The experiment was run on a Dell computer using E-Prime software to create the stimuli, and data were recorded by a Macintosh computer using NetStation software. Onset and offset triggers were created by the E-Prime tool and transferred to NetStation. Impedance was kept below 50 kΩ as recommended for high-input-impedance EGI amplifiers (Ferree et al., 2001; Picton et al, 2000). Data were recorded with an online filter of 0.1 Hz low cut-off (high-pass) and 200 Hz high cut-off (low-pass), with a sampling rate of 500 Hz. Data were stored and transferred to another server for off-line analysis. The Cz electrode was used as reference electrode during the recordings.

2.4 Procedure

When a participant arrived he/she was given the information letter and signed the consent form. The EEG net was prepared in electrolyte solution to ensure good impedance, and the recording equipment was prepared before the participant arrived. Then the net was mounted and the participant was led into the experimental room. The participant was seated in front of screen in a dimly lit room, where he/she was presented with the stimuli. The participant was told to focus on the middle of the screen (see Figure 1) as if he/she was driving a car, and to be mentally aware of the three different speeds of ego-motion. These instructions were given to ensure that the participant was focused on the task at hand.

2.5 Analysis

Brain data analysis

VEP and time-frequency analyses were carried out in BESA 5.3 (Brain Electrical Source Analysis, BESA GmbH). For the VEP analysis the data were divided into epochs of -

300 ms to 600 ms. Eye blink removal was performed semi-automatically (Ille, Berg & Scherg, 2002). All trials and epochs with amplitudes over 200 µV, gradients over 75 µV/sample and signals below 0.1 µV were left out of further analysis. Bad channels were discarded, but no more than 10% (24 channels) in each participant (no more than 5 electrodes in parietal and occipital areas, and no two electrodes adjacent to each other were removed). Average trial contribution for all participants were (out of 75) 71 for low speed (SD: 3.8), 73 for medium speed (SD: 1.5), 71 for high speed (SD: 3.0) and (out of 225) 216 for the static control condition (SD: 6.6).

VEP analysis

Trials were averaged in all participants and re-referenced according to a standardized 27-electrode configuration of the 10-10 international system. Then filters were set to 1.6 Hz low cut-off (high band-pass) to remove slow drift in the data, and 30 Hz high-cut off (low band-pass), notch filter was never changed from 50 Hz and was always on. Components were manually inspected, and peak latency and amplitude values were analysed in SPSS (IBM SPSS Statistics 19). Two two-way repeated measures ANOVAs were conducted to check for significant differences between the three speeds (low, medium, and high) in parietal channels P3 and P4, separately for peak latency and peak amplitude. These two channels were chosen based on previous research reporting activation in area MT/V5 for optic flow type stimuli (Basso et al., 2012; Hayashi, Sugita, Nishida, & Kawano, 2010; Holliday & Meese, 2008, Zeki et al., 1991).

Time-frequency analysis

In addition to peak analysis of VEP components, a time-frequency analysis was carried out in BESA 5.3 (BESA GmbH). The time-domain signal is transformed into the time-frequency domain by complex de-modulation (Papp and Ktonas 1977). A pre-defined 4-shell ellipsoidal head model (Berg & Scherg, 1994; Hoechstetter, 2004) was applied and used to transform data from electrode level to source montage dipoles. A VEP montage was used, which have a higher number of sources mapping the visual area. Sources included in the analysis were (with Talairach coordinates, Talaraich & Tournoux, 1988): visual cortex lateral left (VClL), x=-45.2, y=-57.2, z=6.5, visual cortex lateral right (VClR), x=45.2, y=-57.2, z=6.5, parietal midline (PM), x=0.0, y=-72.3, z=37.0, visual cortex radial left (VCrL), x=-25.6, y=-73.0, visual cortex vertical midline (VCvM), x=0.0, y=-84.9, z=-14.3, and visual cortex radial right (VCrR), x=25.6, y=-73.0, z=4.2.

Time-spectrum evolution (TSE) displays were set from 2 – 30 Hz, and frequency and time sample were set at 1 Hz and 50 ms, while filters were kept at 1.6 low cut-off (high band-pass), and 30 Hz high-cut off (low band-pass). Averaged waveforms were removed, and power (μV^2) was used as the measure unit. The static inter-stimulus interval was used as a control and was also computed separately. For the time-frequency analysis the epoch was set to -100 to 1000 ms. A bootstrapping method was performed in each TSE plot, for each of the participants, to test for significance, and significance level α was set to 0.05.

Paired samples t-tests were conducted in BESA Statistics 1.0 (BESA, GmbH), to test for significant differences between conditions in the time-frequency domain. In this analysis the TSE data from all participants were averaged and analysed together. BESA statistics uses a combination of permutation testing and data clustering (Bullmore et al., 1999; Maris & Oostenveld, 2007; Ernst, 2004) to avoid the multiple comparisons problem. First, data clusters that show a significant effect between conditions are defined. Then, the clusters are put through several permutations, and a new t-test is computed for each permutation and a new cluster value is found. The significance of the initial cluster value is determined based on this new distribution. If the values of condition 1 is lower than the values of condition 2 a negative cluster is found, which shows the direction of the statistical effect. There were 1024 permutations for each t-test (low – static, medium – static, and high - static), frequency ranges and epochs were the same as in the time-frequency analysis.

3.0 Results

3.1 VEP analysis

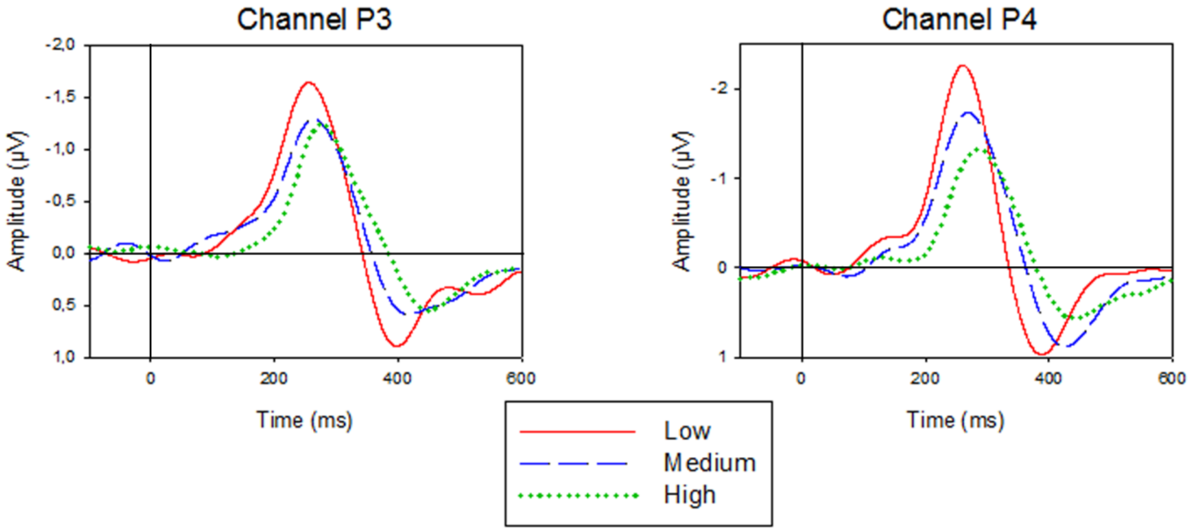

Figure 2 *Grand average VEPs for stimulus speeds low, medium, and high in channels P3 and P4.*

The N2 component had a latency of 246 ms (SD=36) (P3) and 246 ms (SD=30) (P4) at low speed, while it was 254 ms (SD=42) and 272 ms (SD=36) at medium speed, and 265 ms (SD=41) and 292 ms (SD=37) ms at high speed (see Figure 2).

Two two-way repeated measures ANOVAs were conducted, with speed (low, medium, and high) and channel (P3 and P4) as within-subjects factors for peak latency and peak amplitude separately. The ANOVA that measured the effect of speed and channel on latency showed a significant main effect of speed, *F*(2,18)=36.06, $p<0.001$, showing that in both channels latency increased as the speed increased (see Figure 2). There was no significant main effect of channel, *F*(1,9)=1.346, *ns*. Lastly, there was found a significant interaction effect between speed and channel, *F*(2,18)=5.70, $p<0.05$, showing that channel P4 had a greater increase in latency than channel P3.

Peak amplitudes in the parietal channels P3 and P4 were -2.63 (SD=1.06) and -3.30 (SD=1.40) μV at low speed, and -2.27 (SD=0.97) and -2.38 (SD=0.98) μV at medium speed, and -1.34 (SD=1.68) and -2.05 (SD=1.08) μV at high speed (see Figure 2).

The ANOVA that studied the effect of speed and channel on peak amplitude yielded a significant main effect of speed, *F*(2,18)=10.53, $p<0.05$. These results indicate that the amplitude decreased as the speeds increased (see Figure 2). There was no significant main effect of channel, *F*(2,18)=0.932, *ns,* showing that channel had no effect on amplitude, and there was no significant interaction effect between speed and channel, *F*(1,9)=0.838, *ns*.

3.2 Time-frequency analysis

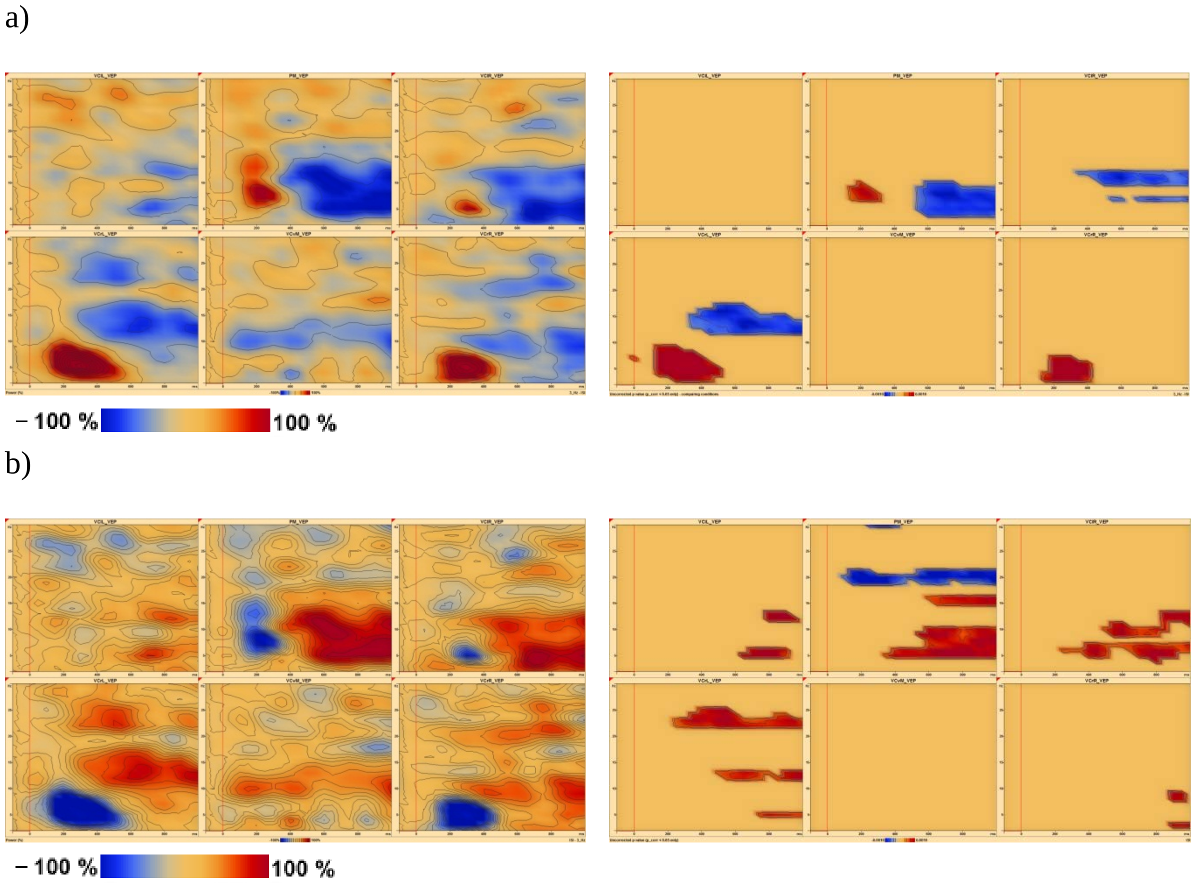

Figure 3 *TSE map (left) and TSE probability map (p<0.05) (right) in the low speed condition (a) and in the static condition (b) for a typical participant, in sources (top left to bottom right): VClL, PM, VClR, VCrL,VCvM, and VCrR. Red line indicate stimulus onset.*

A time-frequency analysis was carried out for the three forward motion conditions and the static condition for all participants. Each of the three forward motion conditions were compared to the static condition (low – static, medium – static, and high – static), while the static condition was compared to the low speed condition. See Figures 3a and b for results of one typical participant for TSE maps for the low speed and the static condition, respectively.

Participants showed induced theta-band synchronization from 200 – 400 ms after stimulus onset followed by induced alpha-band de-synchronization from 400 ms to, and beyond, stimulus end (see Figure 3a for the low speed condition). The medium and high speed conditions showed similar results (see Appendix A for TSE plots for all participants and Appendix B for TSE probability maps for all participants). The static condition (Figure 3b) showed the opposite oscillations, i.e. induced de-synchronization in the theta-band followed by synchronization in the alpha-band.

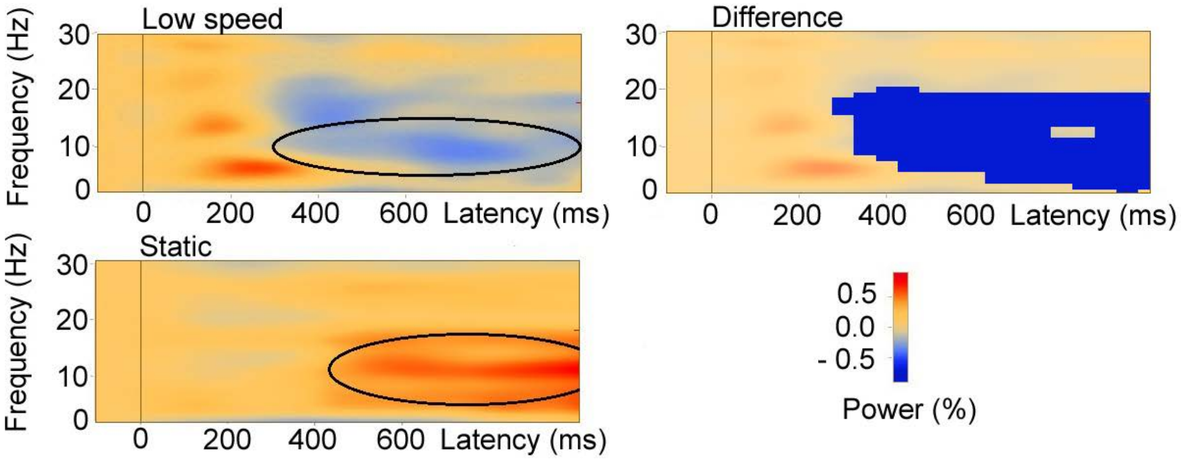

Figure 4 *Averaged TSE plots of all participants in the PM source, where top left is for the low speed condition, bottom left is for the static condition, and top right is the area of significant difference (p<0.05) between low speed and the static condition. Areas of de-synchronization (blue colours) and synchronization (red colours) are shown in the low speed and static condition. The blue area (top right) indicates that the difference (low speed minus static) was negative, meaning that the cluster values in low speed (black oval in top left) were lower than the cluster values in the static condition (black oval in bottom left).*

Several two-tailed t-tests were carried out in BESA Statistics (v 1.0). The time-frequency analyses from all participants were averaged and the three different motion conditions were compared to each other, as well as to the static control condition. No significant differences between the three speeds were found when they were compared to each other, indicating a similarity in the induced response to the three different motion conditions. Then, low, medium, and high speeds were each compared to the static condition. There were no significant differences between the de-synchronization in the theta-band in the motion conditions and the synchronization in the theta-band in the static condition. However, significant differences were found between the de-synchronization in the alpha-band in the motion conditions (low, medium, and high) and the synchronization in the alpha-band in the static condition in the PM source. Paired-samples t-tests showed significant differences between low speed and the static condition ($p<0.05$), between medium speed and the static condition ($p<0.05$), and between high speed and the static condition ($p<0.005$). The maximum activity was found in the alpha band, in the time range from 600 – 800 ms, while there was activation from 300 ms to stimulus end. The significant differences were found in the frequency ranges between 5 and 17 Hz in time ranges from approximately 300 ms to stimulus end (see Figure 4, and Appendix C for medium and high speed) in all conditions, showing that the motion conditions had significantly lower power compared to the static condition, which showed higher power (synchronization) in the PM source.

4.0 Discussion

This high-density EEG study was conducted to investigate brain responses to three different speeds of forward motion. The stimulus was a road simulated by poles moving from near the centre of the screen and out towards the edges of the screen, creating an ecological simulation of an optic flow field. Scalp potentials in parietal channels P3 and P4 were investigated for the three different speeds (low, medium, and high) of forward motion.

We found significant differences between the three motion conditions (low, medium, and high) in both channels (P3 and P4) in the VEP analyses. The peak latencies significantly increased as the speeds increased, while the amplitude decreased as the speeds increased. The time-frequency analysis showed theta-band synchronizations followed by alpha-band de-synchronizations as a response to the three forward motion conditions, while the static condition showed opposite theta-band de-synchronizations followed by alpha-band synchronizations. However, theta band (de-)synchronizations were not significantly different between the three different speeds, or between the three different speeds and the static control condition. The PM source showed significant differences between the alpha de-synchronization in response to three speeds and the alpha synchronization in response to the static control condition.

The N2 component in occipital and parietal areas is linked to motion perception (Probst, Plendl, Paulus, Wist & Scherg, 1993; van der Meer et al., 2008, Morrone et al., 2000), and this component is modulated by the direction, velocity, luminance, and contrast of the stimulus (Heinrich, 2007; Müller & Göpfert, 1988; Schlykowa, van Dijk & Ehrenstein, 1993; Bach & Ullrich, 1993). Our results, which indicated an increase in latency and decrease in amplitude for increasing speeds of simulated ego-motion, are the opposite of the results found in some studies, reporting decreasing latencies for increasing speeds (Maruyama et al., 2002), and the opposite of what Heinrich (2007) concluded to be the most common finding. One study showed an increase in latencies for stimulus speeds over 100 °/s (Kawakami et al., 2002), using vertical checkerboard stimuli. These latency findings are the same as found in the current study and indicate that increasing speeds were processed in the same manner as the stimulus speeds used by Kawakami et al. (2002). However, the study of Kawakami et al. (2002) used non-gradient stimuli without perspective, which makes a direct comparison difficult.

The latency results observed in the present study, i.e. different latencies for three different speeds of simulated forward motion could reflect increased processing times for more complex stimuli or faster simulated speeds. Luck (2005) argued that one of the advantages of ERPs is that they are an online measurement of cognitive information processing, but Hood (2001) noted that the underlying activity is associated, not causally linked, with the behaviour. When we move at higher speeds the areas involved in motion processing might need more time to process the incoming information, indicating that the faster we move through an environment the more difficult it becomes to process the incoming information. Van der Meer at al. (2008) found higher latencies for random visual motion than for structured optic flow, and argued this was because it was easier to detect the coherence in structured optic flow.

There was found an interaction effect between channels P3 and P4, which shows that latencies in channel P4 had a significantly greater increase over the three different speeds compared to channel P3. This interaction effect could suggest that the right hemisphere is more involved in the processing of this type of stimulus. Right lateralization for motion stimuli was also found in a study by De Jong, Shipp, Skidmore, Frackowiak, and Zeki (1994), who found that the right latero-posterior precuneus (superior parietal lobe) was an important contributor to the processing of optic flow stimuli (fed by area V3).

There was found a significant main effect of amplitude showing that amplitude decreased with increasing speeds. Amplitude reflects the number of synchronously active neurons (Elul, 1972; Pfurtcheller & Lopes da Silva, 1999). Low amplitudes indicate fewer neurons firing in synchrony, and therefore fewer neurons attuned to the particular condition, while high amplitudes reflect a higher number of neurons firing in synchrony. This would seem to indicate that there are more neurons firing in synchrony in response to the lowest speed, and that most of the neurons in the motion area are attuned to lower velocities. Indeed, Liu and Newsome (2003) found that neurons are clustered according to preference of speed. The present findings thus seem to indicate that there are more neurons responsive to the lower speed condition and that they are firing in synchrony to produce higher amplitudes.

EEG is not as spatially accurate as other methods (PET, fMRI) (Luck, 2005), so it is difficult to pinpoint the exact area that responds to our optic flow stimuli. However, previous studies (Basso et al., 2012; Liu and Newsome, 2003; Liu & Newsome, 2005; Hayashi, Sugita, Nishida, & Kawano, 2010, Zeki et al., 1991) have shown contributions from areas such as MT/V5, and also the MST area has been shown to process optic flow stimuli (Duffy & Wurtz, 1997; Duffy, 1998; Holliday & Meese, 2008). Thus, studies on visual motion using stimuli both without perspective (e.g., checkerboard gratings) and with perspective (optic flow) show that there are several areas responsible for visual motion processing, but for optic flow stimuli, higher processing in areas such as MST (Phinney & Siegel, 2000; Merchant, Battaglia-Mayer & Georgopoulos, 2001, Merchant, 2004; Liu & Newsome, 2003) and the superior parietal lobe mentioned above (De Jong et al., 1994) is also of great importance.

In short, the present findings could indicate that when we move at increasing simulated speeds in a virtual environment, the brain seems to take more time to process the incoming optic flow information, and the brain's motion area seems to be more attuned to the lower speed.

Differences between earlier visual motion studies and the current study are higher N2 latencies, where earlier studies with adults generally found latencies of approximately 150-250 ms (Kuba & Kubová, 1992; van der Meer et al., 2008) while this study showed latencies of up to 292 ms. These latencies could indicate that the stimulus in the current study was more difficult to process, and this could indicate that the current speed stimuli are in general more complex than checkerboard and grating stimuli, and previously used optic flow stimuli.

In addition to VEP analysis, a time-frequency analysis was also carried out, to study changes in brain oscillations in response to the three different speeds of visual motion. In the TSE analysis the static control condition was compared with the three speeds. Looking at brain oscillations in the temporal-spatial domain has become more common in recent years, allowing for analysis of non-phase-locked responses (Pfurtscheller & Lopes Da Silva, 1999). The current results showed short theta synchronizations in occipital and parietal sources, followed by de-synchronizations in the alpha-band in the same sources. However, there were found only significant differences between alpha-band synchronization and de-synchronization in the PM source. There were no significant differences *between* the three visual motion conditions in the TSE analysis. The three different speed conditions are basically the same stimuli, in that they all show the exact same scene, only moving at low, medium, and high speeds. So it may be that the same area is responsible for the processing of the three different speeds, and that the observed alpha de-synchronization reflects a general cognitive processing of stimuli, and attention, found in parietal areas (Pfurtscheller, Neuper & Mohl, 1994). Differences lie in the perceived self-motion, i.e. in the speed the participants experience, not in the environment the participants find themselves in, and the differences between the three speeds are only seen in the VEP analysis of the N2 component. If the alpha de-synchronizations reflect the general processing of the three speeds of visual motion, then VEP latency and amplitude reflect the processing time and load, respectively.

Occipital and parietal de-synchronizations in alpha-band frequencies are thought to reflect an activated state (Pfurtscheller, Neuper & Mohl, 1994; Klimesch, 1999), and this fits well with the present findings. There was a long alpha de-synchronization in the PM source in response to the three different speeds, followed by synchronization in response to the static condition, which is related to a deactivated or resting period. The activated state is thought to reflect the processing of visual stimuli. Pfurtscheller, Neuper and Mohl (1994) reported two different alpha bands: a lower one reflecting visual processing situated in occipital areas, and a higher one reflecting cognitive processes and attention situated in parietal areas. The participants' alpha de-synchronizations were, however, too variable and the data not accurate enough to identify whether they were higher or lower alpha waves. Coupled with findings of visually evoked N2 components, the induced oscillations might, however, indicate visual motion processing.

The alpha de-synchronizations may reflect the fact that the participants were in an attentive state, while the following alpha synchronization may reflect that the participants relaxed and did not pay much attention during the 3 s static condition. The participants were explicitly told to pay attention to, and be aware of the three different speeds.

As can be seen from Appendices A and B, there are differences between participants, not all show oscillatory activity in the same sources. The most common source, which shows activation in almost all participants, is the PM source. However, there was greater variance in the other sources. This is likely to be a result of the fact that we used an average adult head model for the sources, and this, included with individual differences between the participants, is most likely the reason for the differences seen.

In conclusion, a marked difference was found in VEP components between the three visual motion conditions (low, medium, and high speed). The N2 peak latency increased as the stimulus speeds increased, and this could indicate that the lower speeds were easier to process, because they were less complex. Amplitude decreased as the speed increased, and this was assumed to occur because fewer neurons respond to higher stimulus speeds, producing lower amplitudes. These differences were interpreted to mean that the amplitude decreased because the motion sensitive areas are less sensitive to higher speeds.

In the induced oscillatory activity a difference was found between the three different motion conditions and the static condition, but not between the motion conditions per se. The de-synchronized alpha activity in the PM source was thought to be a result of general visual processing, reflecting an activated state. The alpha-band synchronizations observed in the static period between the motion conditions were thought to reflect a resting, or deactivated period.

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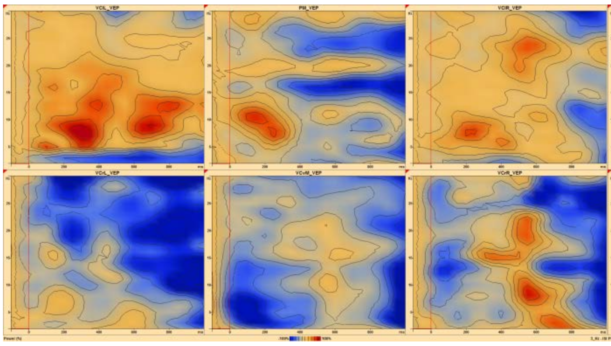
Appendix A

TSE plots from all participants A-J in the low,medium,and high speeds, and the static condition. Blue areas show decrease in induced oscillations (de-synchronizations) and red areas show increase in induced oscillations (synchronizations). Epochs are set from -100 to 1000 ms, range 2 – 30 Hz, and measure unit was power (µV^2). Theta (4-7.5 Hz) synchronizations and alpha (8-13) de-synchronization can mostly be seen in the radial sources in the visual cortex, and parietal midline sources in the three different speeds (low, medium, and high,), but there is also activation in the lateral sources in the visual cortex. Theta (4-7.5 Hz) de-synchronizations and alpha (8-13) synchronization can be seen in similar sources as the three motion conditions, in the static condition. Sources used are: from top left to bottom right): VClL, PM, VClR, VCrL,VCvM, and VCrR. Red line indicate stimulus onset.

Low

A



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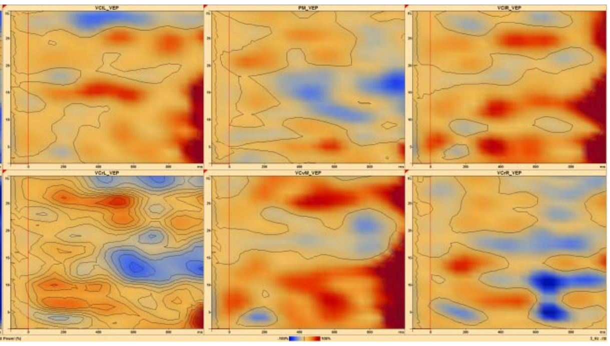

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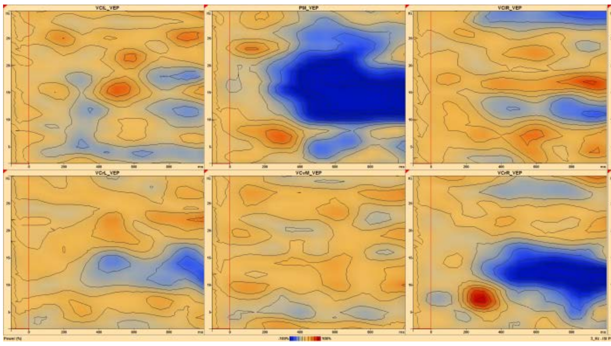

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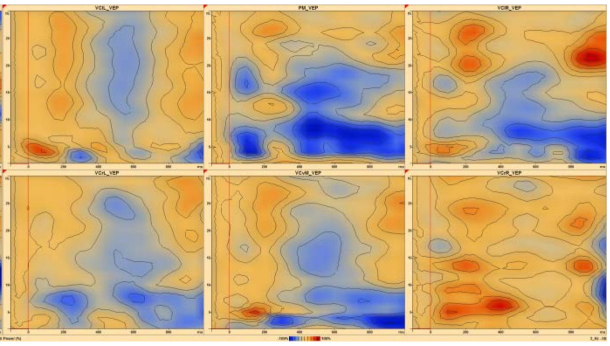

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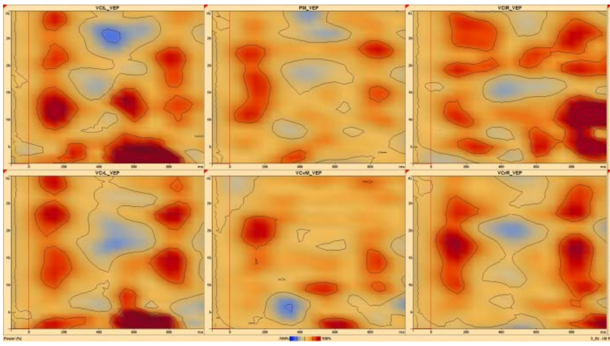

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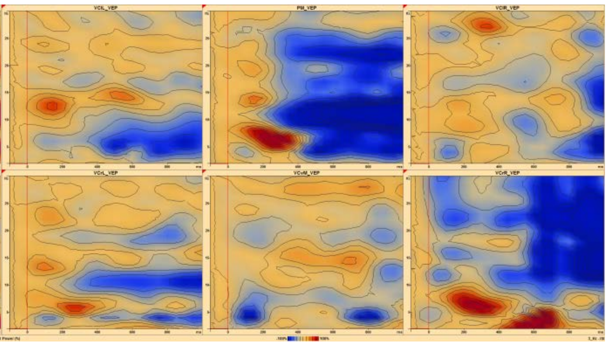

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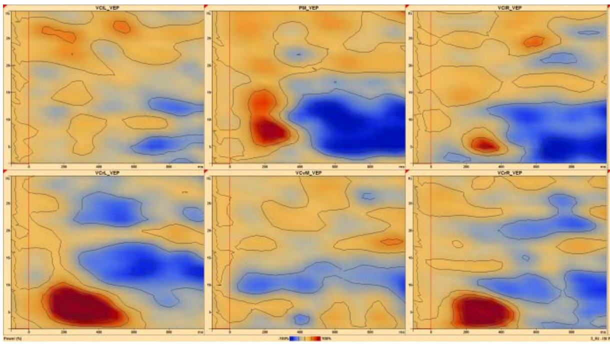

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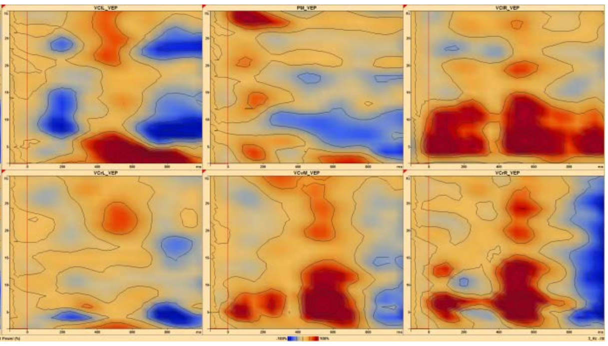

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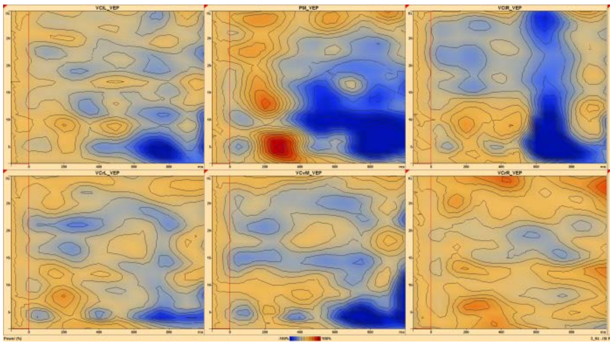

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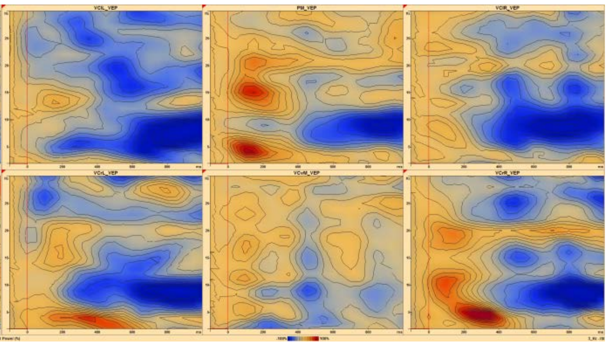

Medium

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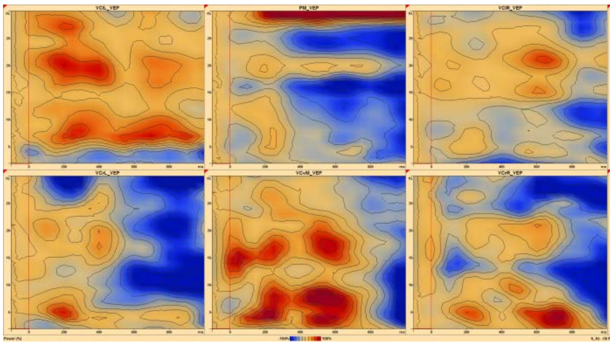

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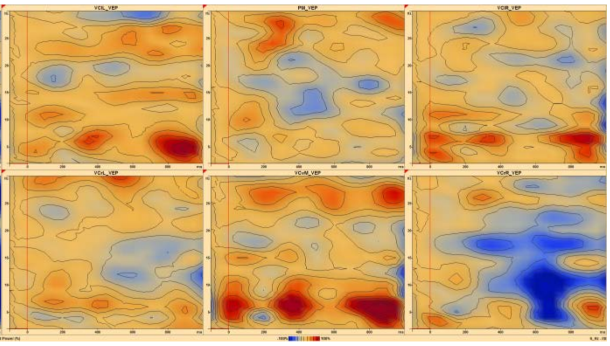

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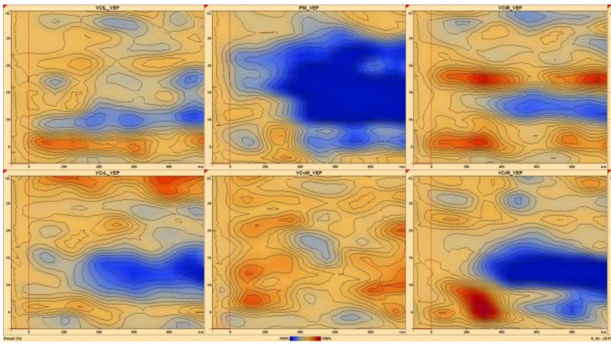
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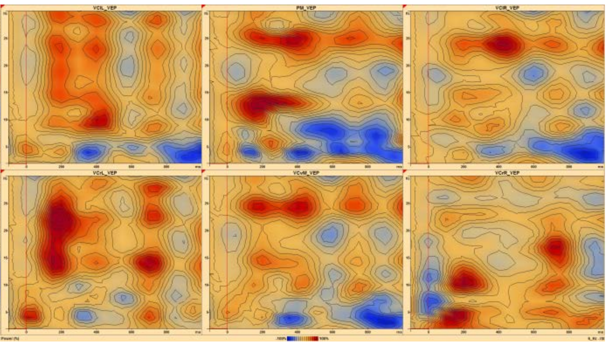
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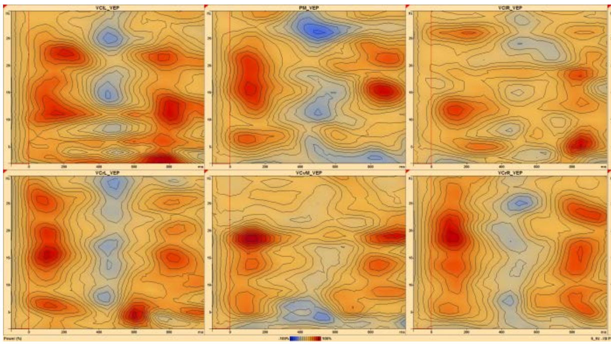
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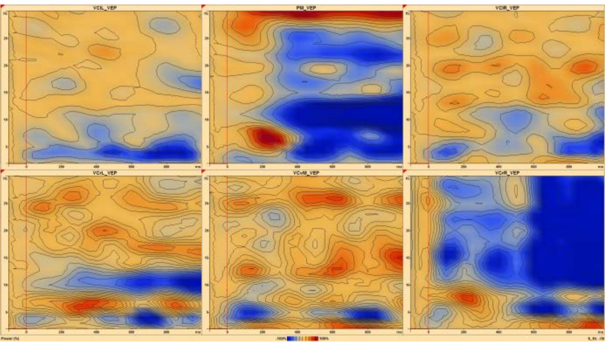
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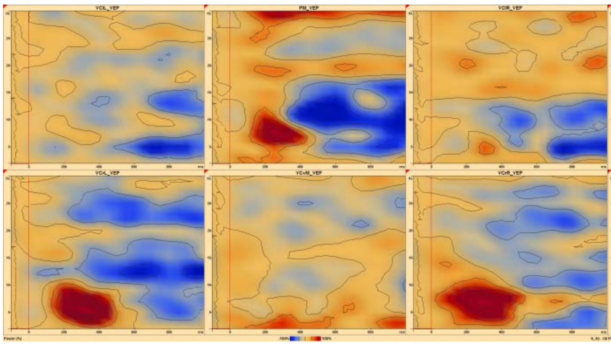
G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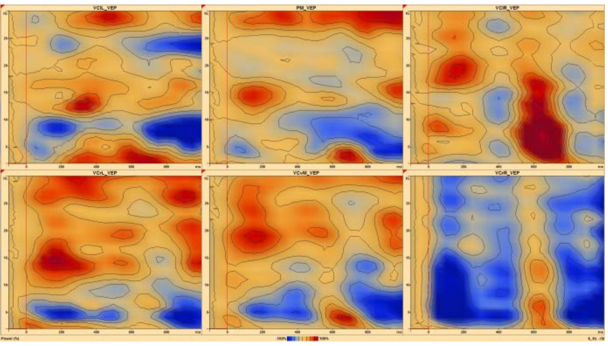
H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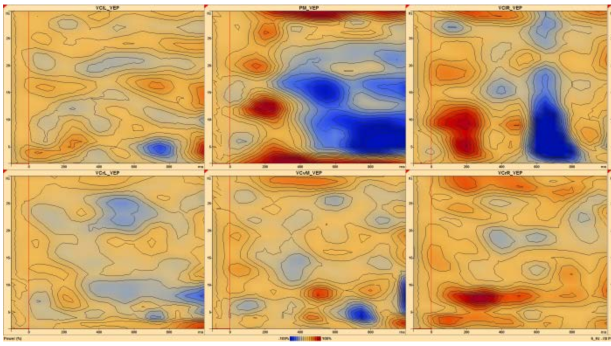
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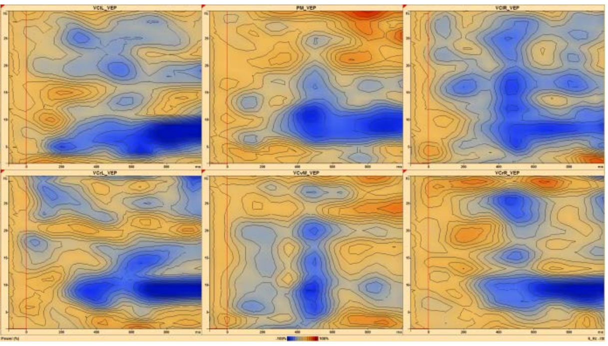
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High

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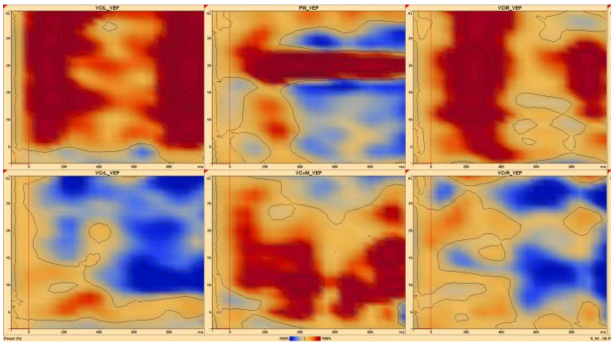
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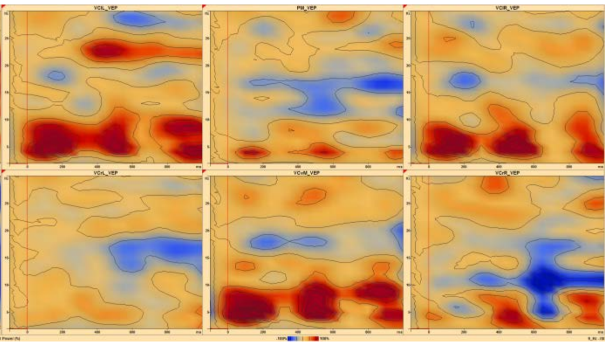
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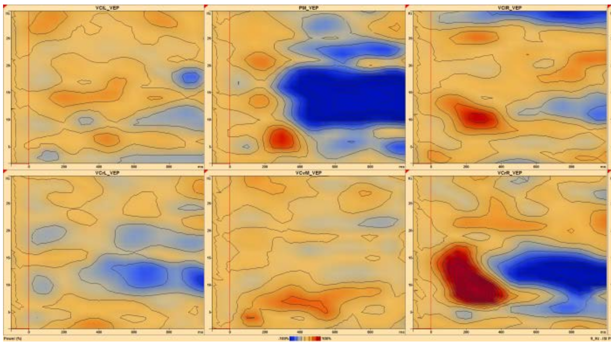
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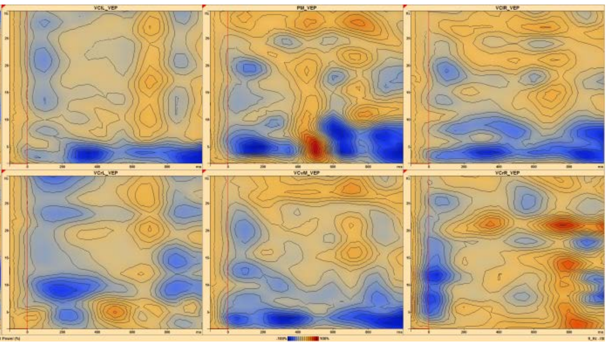
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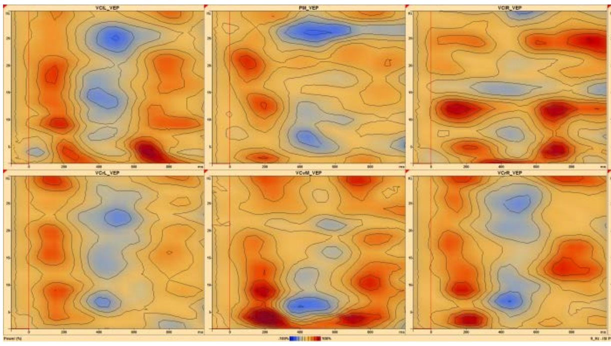
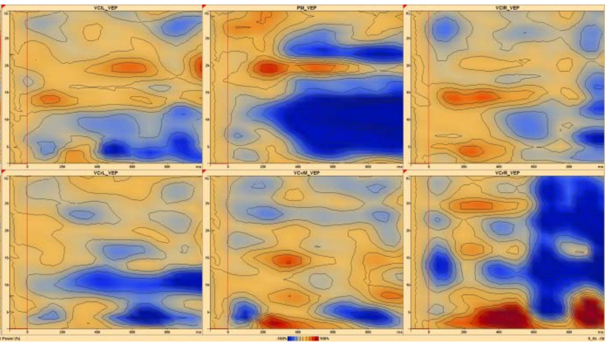
VCrR_VEP
-100%
100%

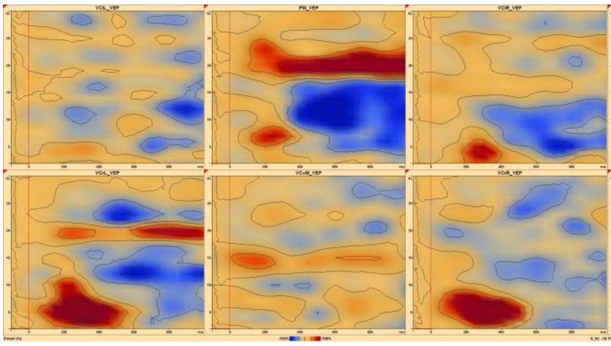
E


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
Power (%)
-100%
100%

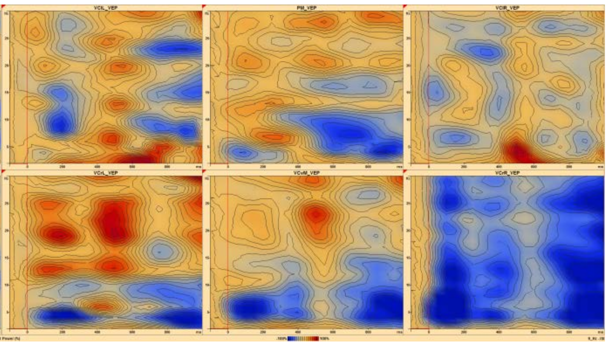
F


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
-100%
100%

G



H



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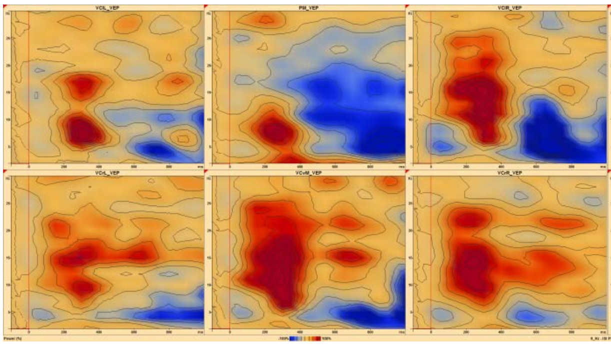

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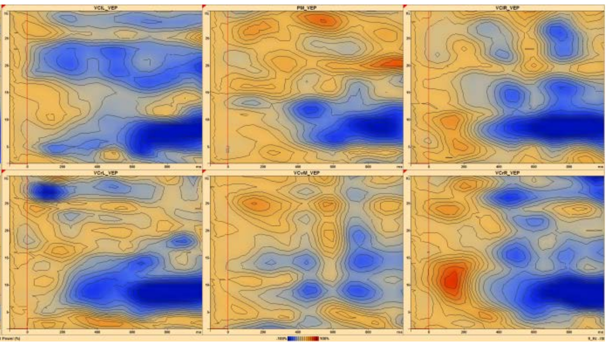
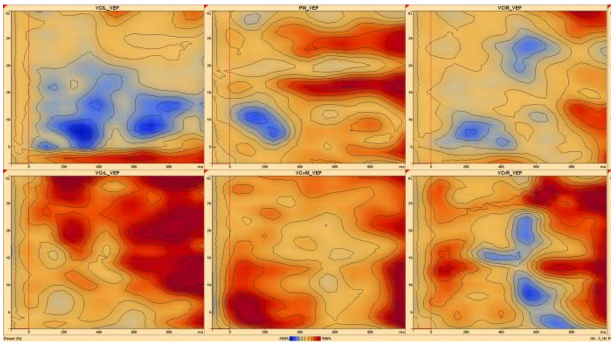
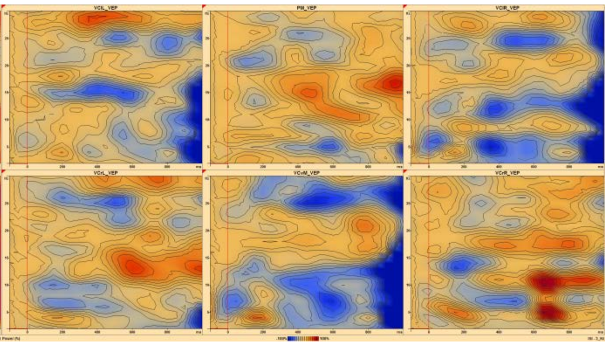


Static

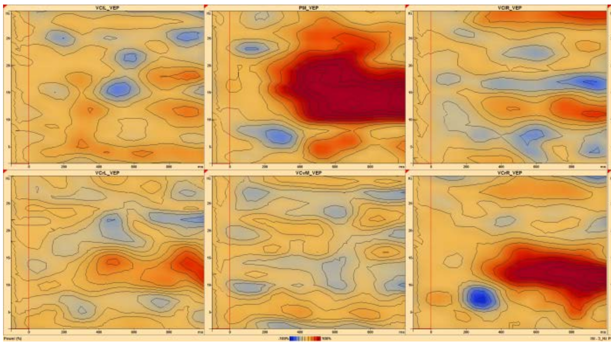
A



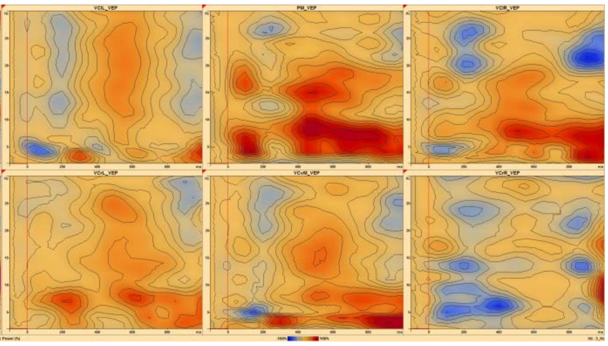
B



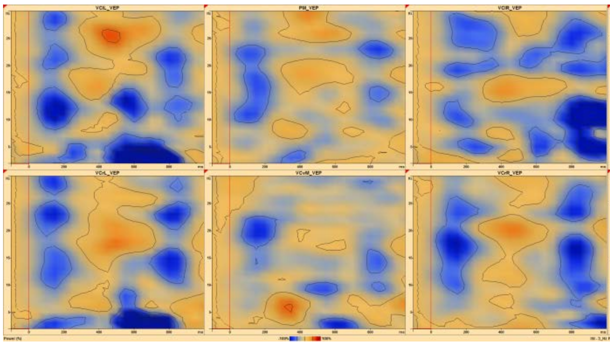
C



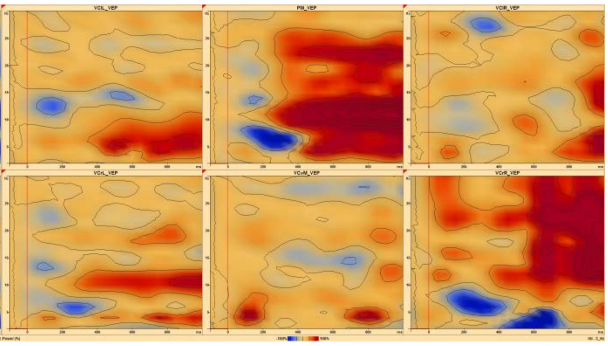
D



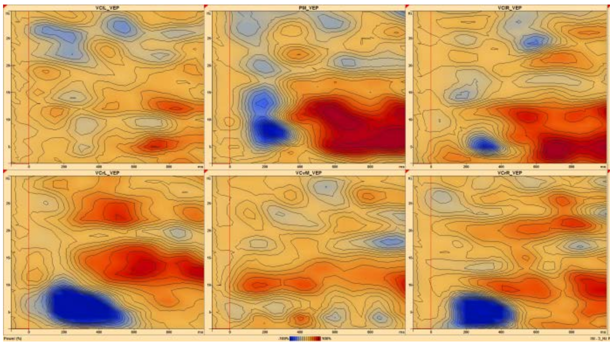
E


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
Power (%)
-100%
100%
ms

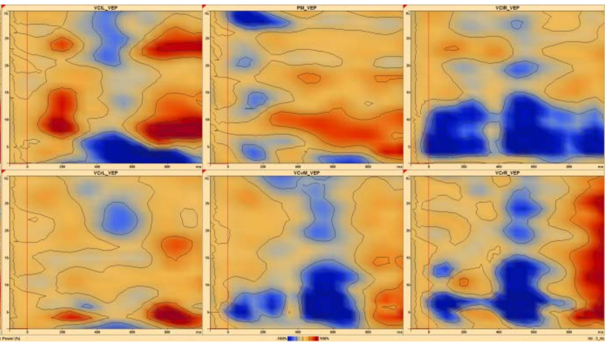
F


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
Power (%)
-100%
100%
ms

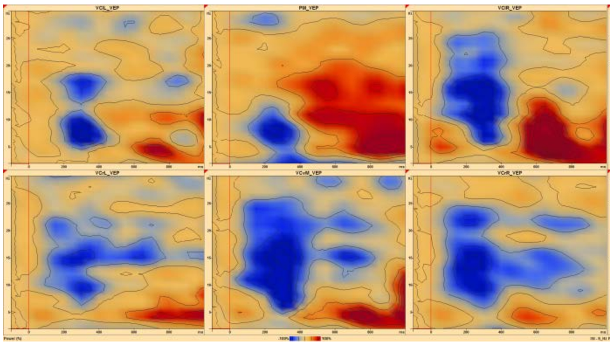
G


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
Power (%)
-100%
100%
ms

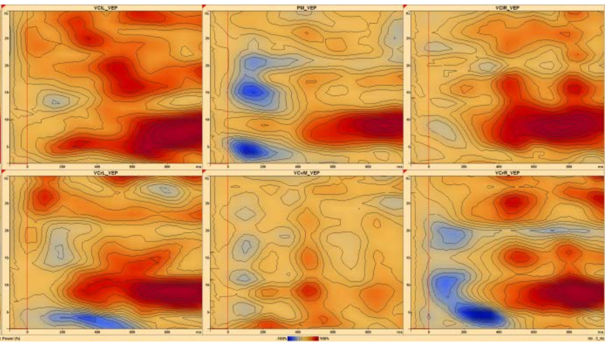
H


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
Power (%)
-100%
100%
ms

I


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
Power (%)
-100%
100%
ms

J


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
Power (%)
-100%
100%
ms

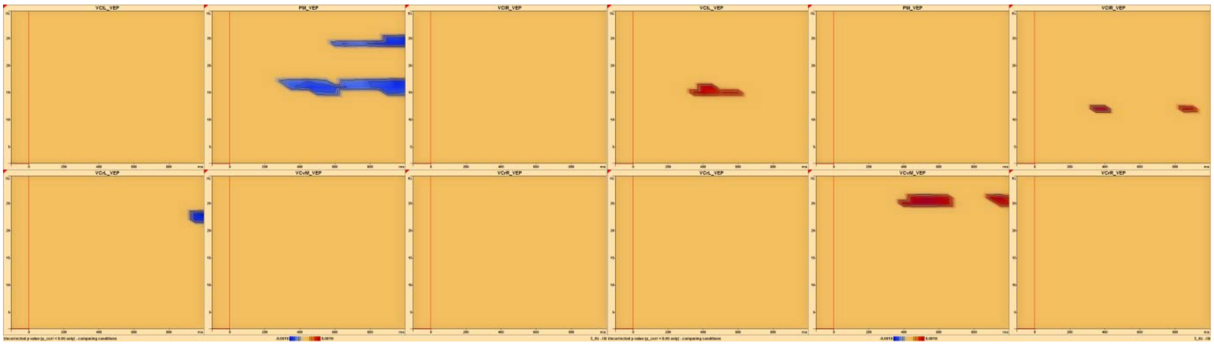
Appendix B

TSE probability maps (p<0.05) from all participants A-J in the low,medium,and high speeds, and the static condition. Blue areas show significant decrease in induced oscillations (de-synchronizations) and red areas show significant increase in induced oscillations (synchronizations). The three different forward motions (low, medium, and high) were compared with the static condition, and the static condition was compared with the low speed condition. Theta (4-7.5 Hz) synchronizations and alpha (8-13) de-synchronizations can mostly be seen in the radial sources in the visual cortex, and parietal midline sources in the three different speeds (low, medium, and high,), but there is also activation in the lateral sources in the visual cortex.. Theta (4-7.5 Hz) de-synchronizations and alpha (8-13) synchronization can be seen in some sources in the static condition. Epochs are set from -100 to 1000 ms, range 2 – 30 Hz. Sources used are: from top left to bottom right): VClL, PM, VClR, VCrL,VCvM, and VCrR. Red line indicate stimulus onset.

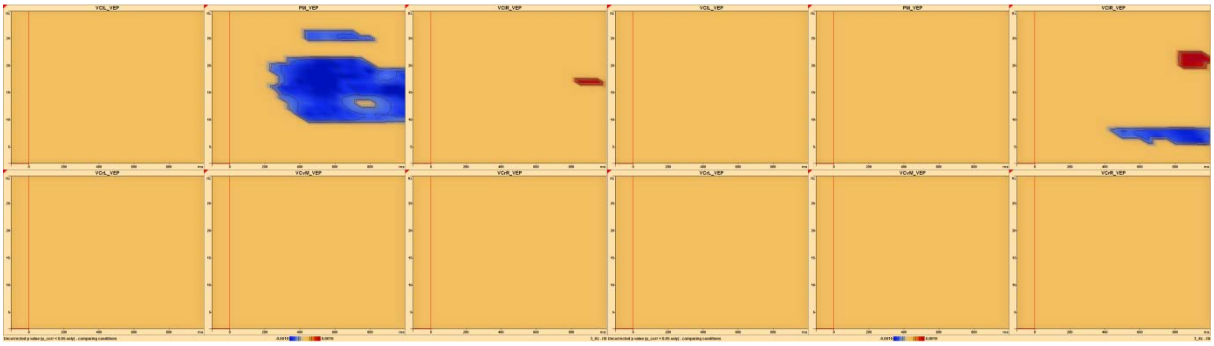
TSE Statistics

Low

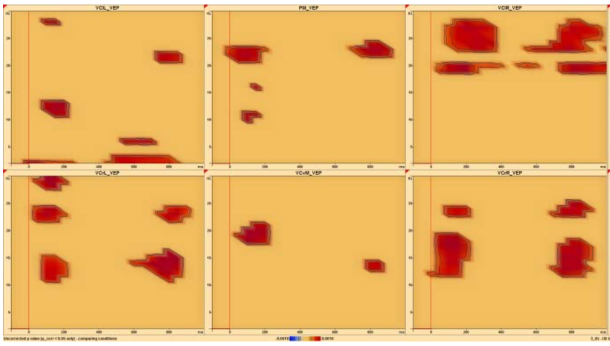
A B



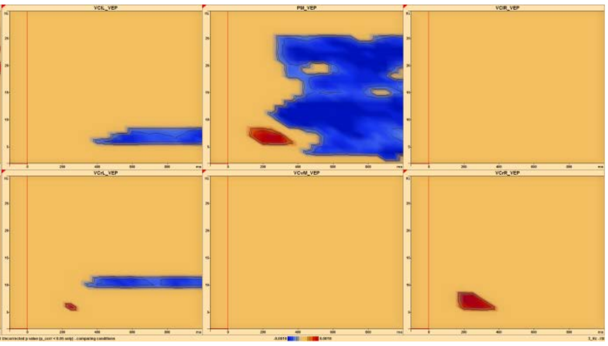
C D



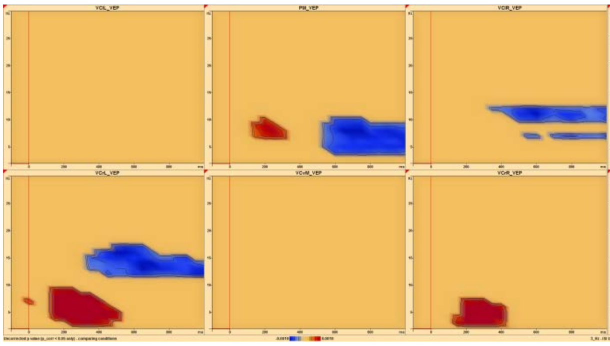
E


VClL_VEP
PM_VEP
VClR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

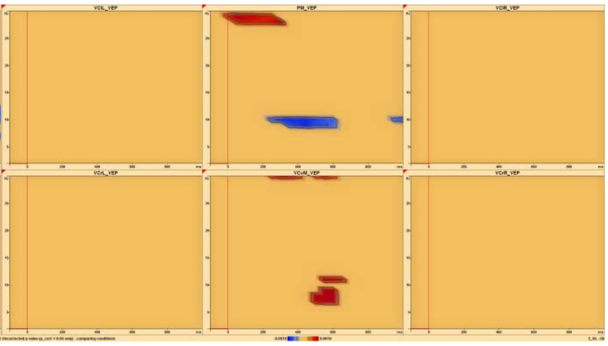
F


VClL_VEP
PM_VEP
VClR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

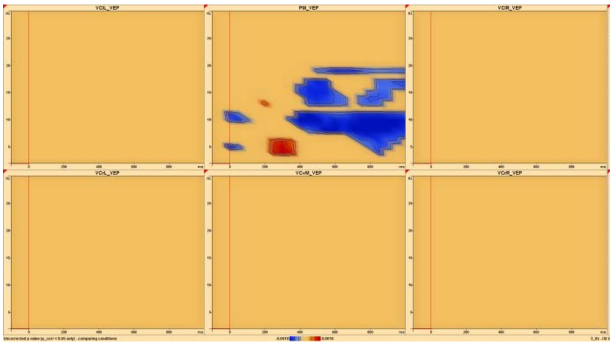
G


VClL_VEP
PM_VEP
VClR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

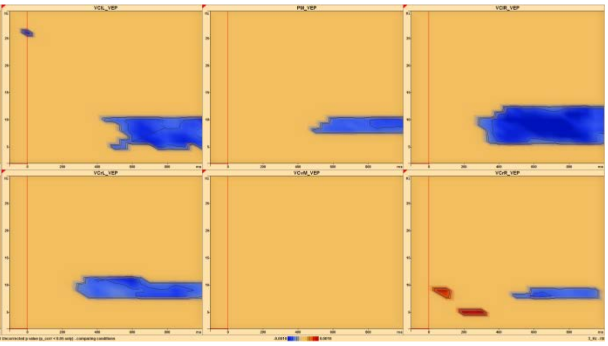
H


VClL_VEP
PM_VEP
VClR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

I


VClL_VEP
PM_VEP
VClR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

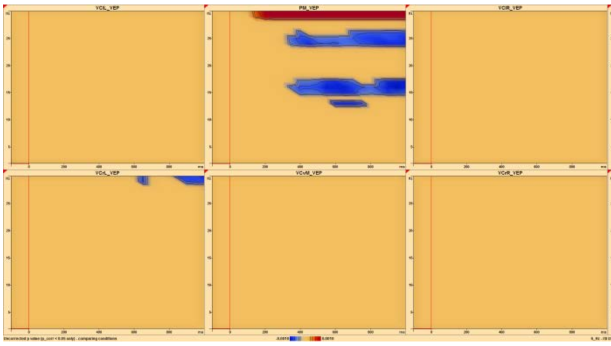
J


VClL_VEP
PM_VEP
VClR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

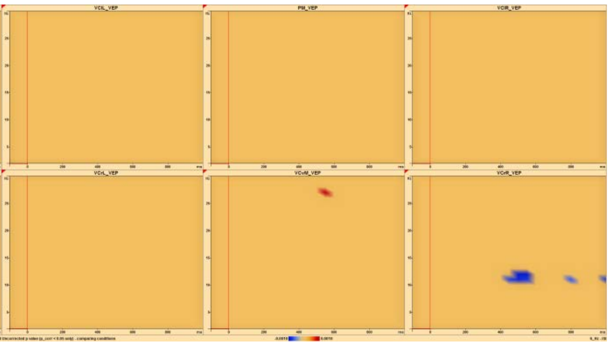
TSE Statistics

Medium

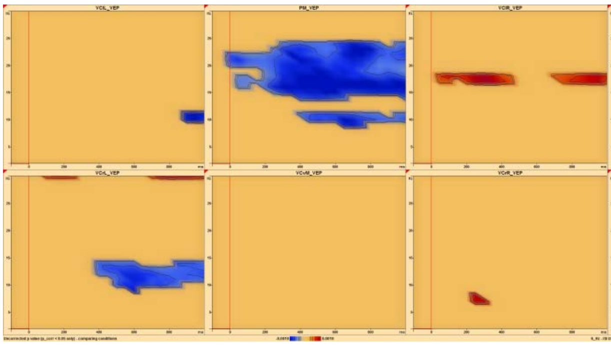
A



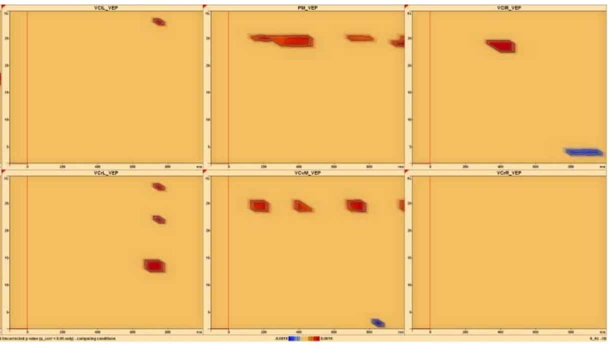
B



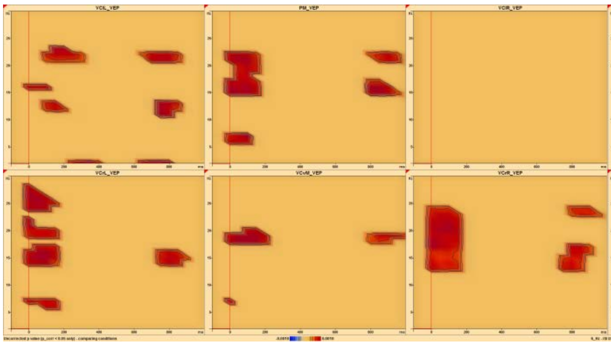
C



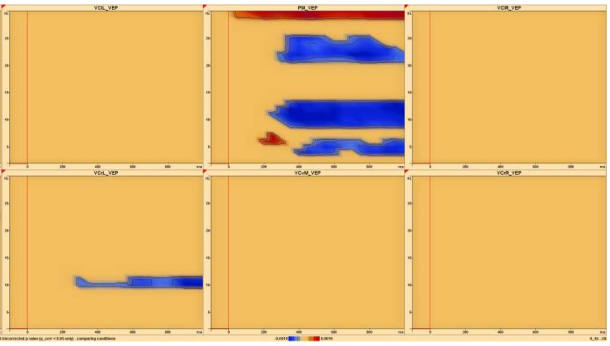
D



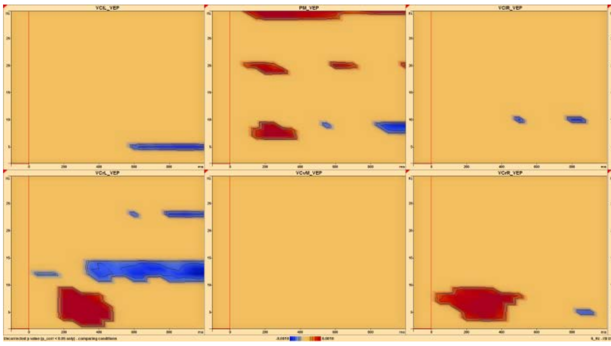
E



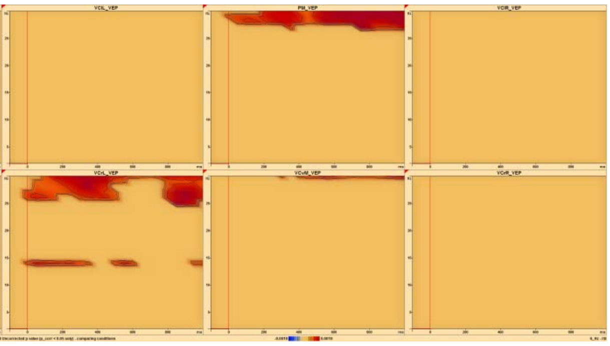
F



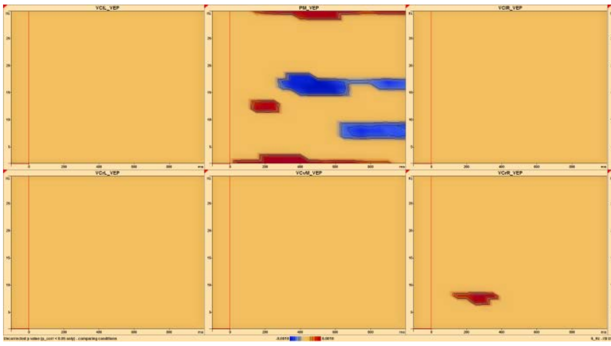
G



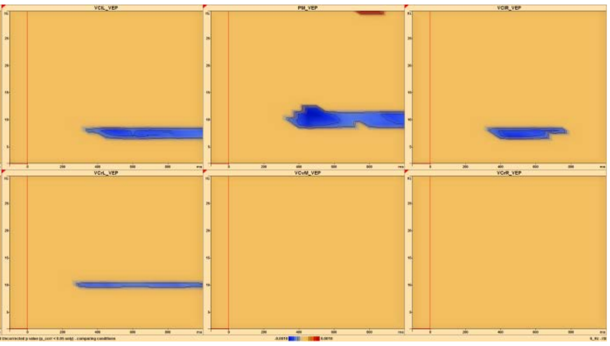
H



I



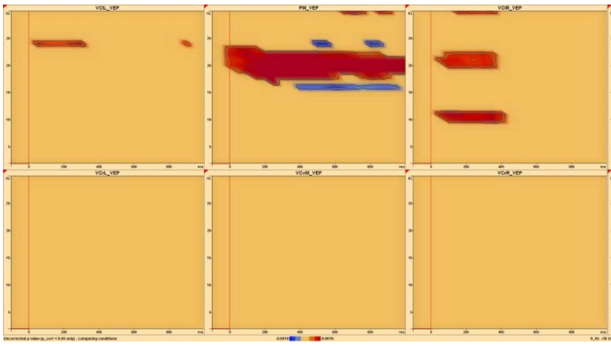
J



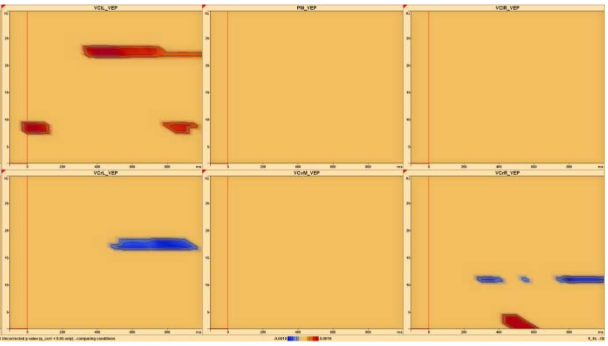
TSE Statistics

High

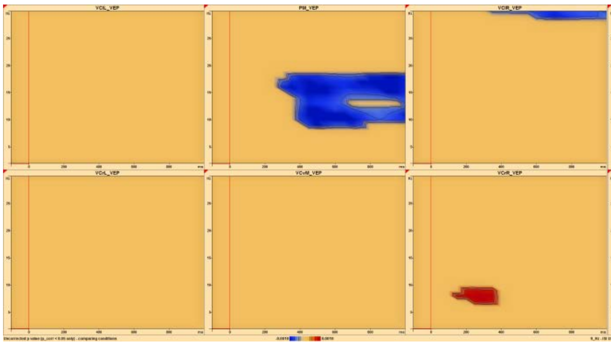
A



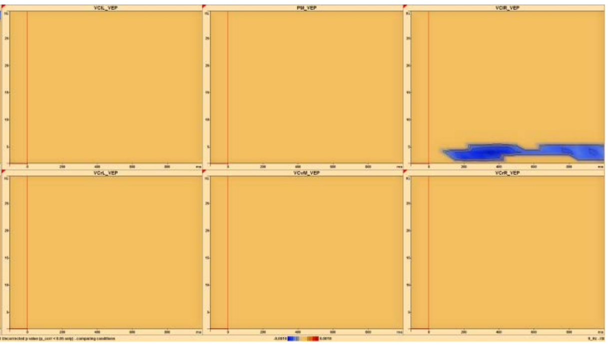
B



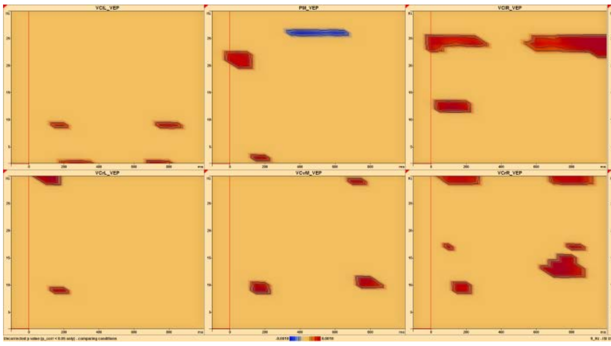
C



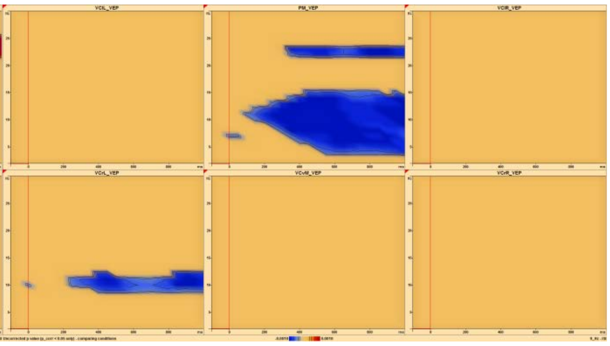
D



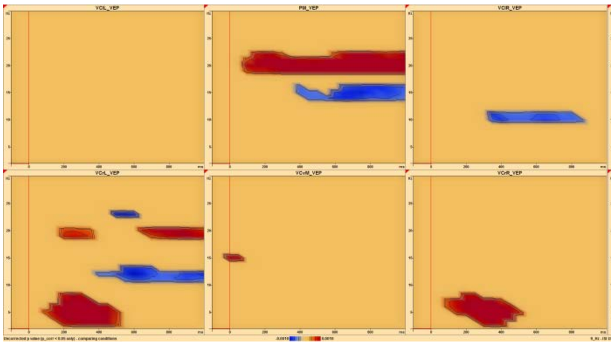
E


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
-0.0010
0.0010

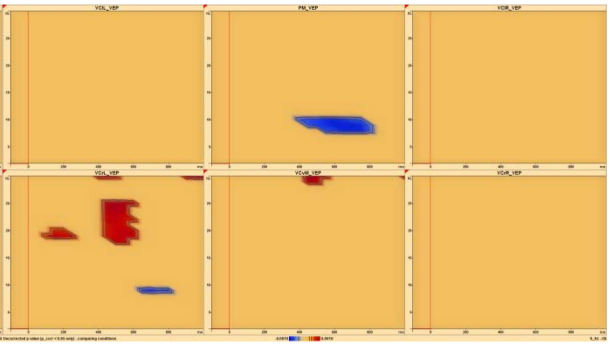
F


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

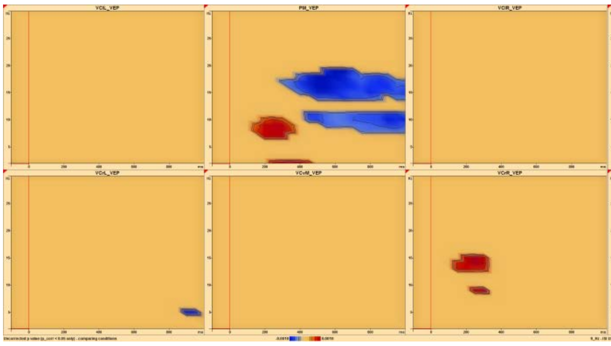
G


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

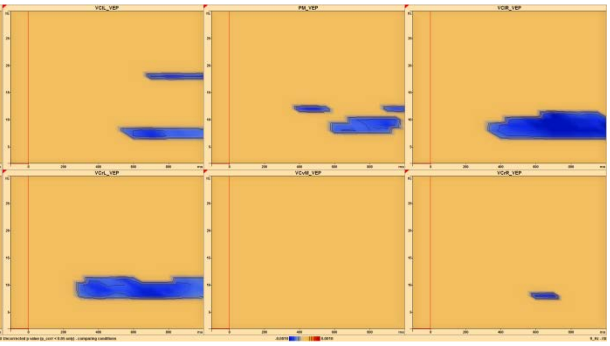
H


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

I


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

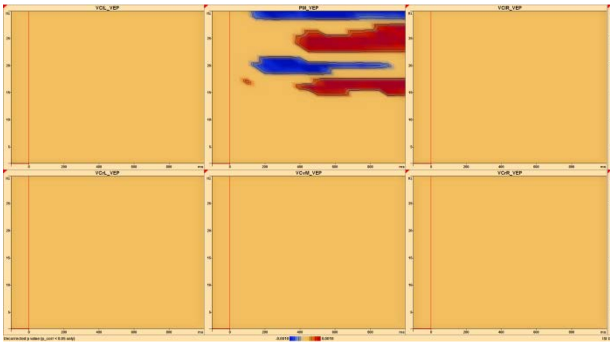
J


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP

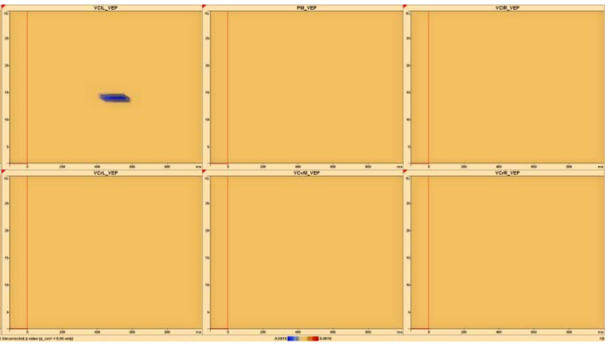
TSE Statistics

Static

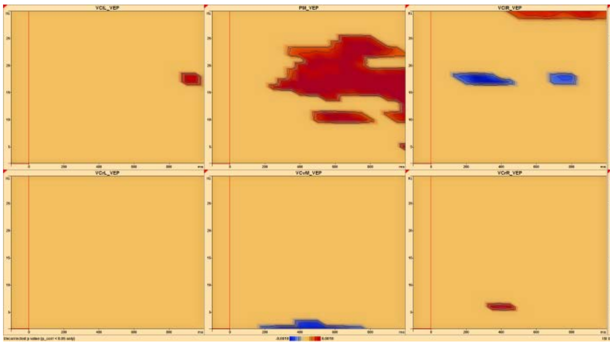
A



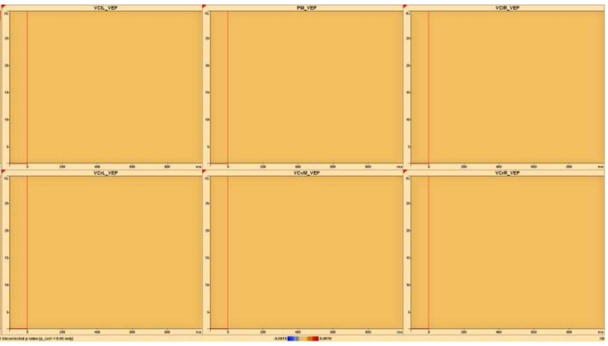
B



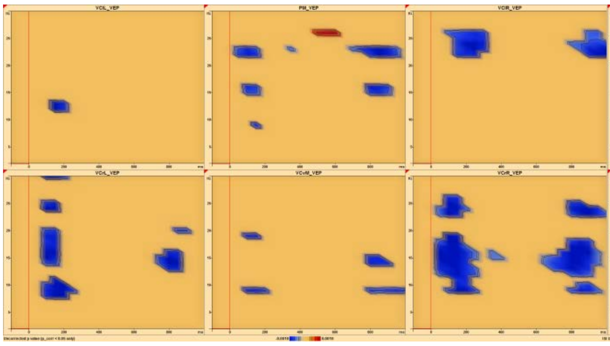
C



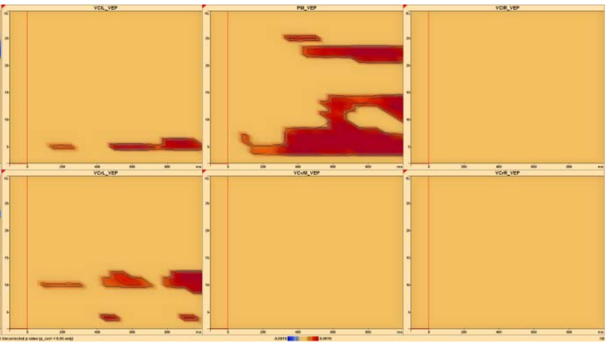
D



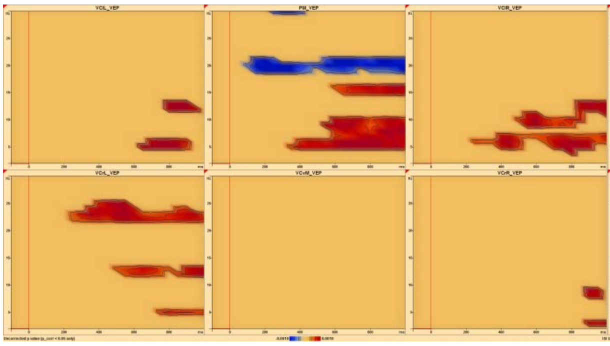
E



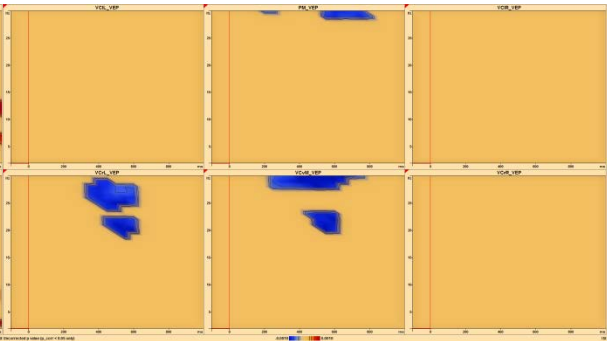
F



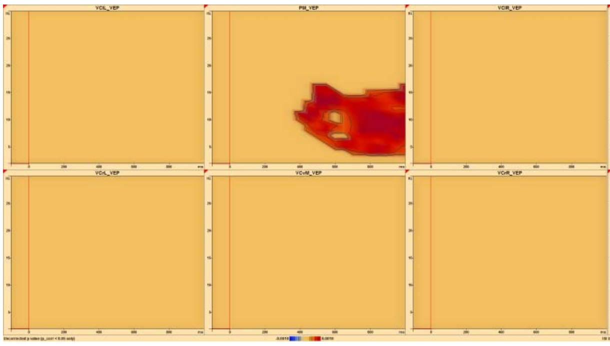
G


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
ms
Uncorrected p values (p_corr < 0.05 only)
-0.0010
0.0010

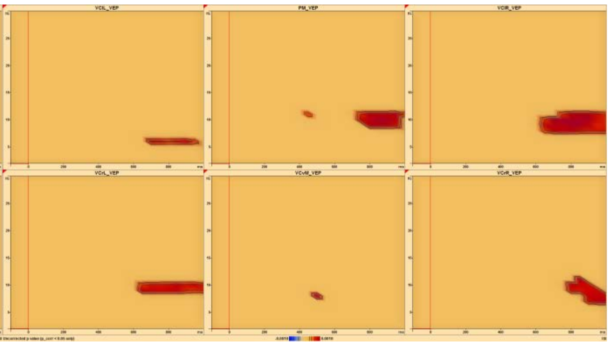
H


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
ms
-0.0010
0.0010

I


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
ms
-0.0010
0.0010

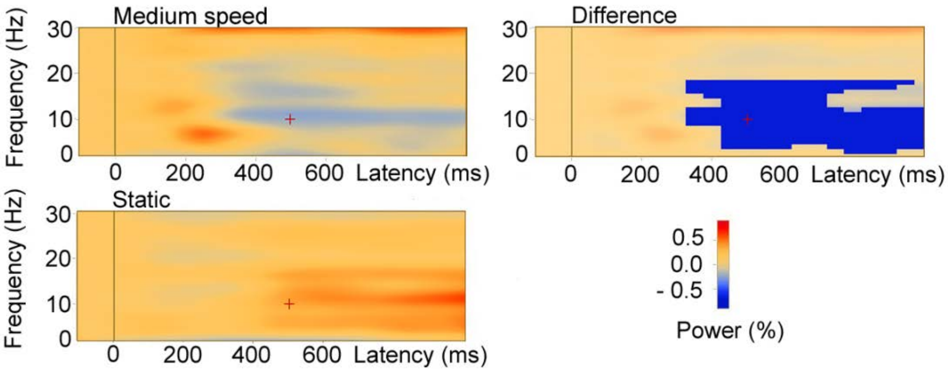
J


VCIL_VEP
PM_VEP
VCIR_VEP
VCrL_VEP
VCvM_VEP
VCrR_VEP
ms
-0.0010
0.0010

Appendix C

Averaged TSE plots of Medium, and High and static condition, and area of significant difference, $p<0.05$ in the Medium condition and, $p<0.005$ in the High condition in the PM source. Medium and High conditions show alpha de-synchronizations (8-13) from approximately 300 ms after stimulus onset to, and beyond, end of epoch, while static conditions show alpha synchronizations (8-13) from approximately 400 ms after stimulus onset, to, and beyond end of epoch. Difference shows area of significant difference between motion conditions and the static condition from approximately 300 ms after stimulus onset, to, and beyond end of epoch in speeds from approximately 2-4 Hz to 17-20 Hz. Epochs are set from -100 to 1000 ms, range 2 – 30 Hz, and measure unit was power (μV^2).

Medium, speed, Static, and area of significant difference



High speed, Static, and area of significant difference