A high-density EEG study of differences between two speeds of forwards and backwards ecological motion in adult participants

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Acknowledgments

Abstract

A high-density EEG study was carried out to investigate the evoked and induced activity caused by an optic flow stimulus simulating ego-motion. The optic flow stimulus consisted of a road with poles on both sides and movement was simulated both forwards and backwards at two different speeds, with a static condition in between movement conditions. The aim was to analyze the N2 component of the visually evoked potentials and the induced oscillatory activity caused by the stimulus, in the occipital and parietal regions of the cortex.

N2 peak latencies in parietal channels P4, PO4, POz and P2 in the low speed motion conditions were significantly lower than in the high speed motion conditions. This increase in N2 peak latencies was thought to reflect that the processing of simulated ego-motion at low speeds is easier than simulated ego-motion at higher speeds.

The analysis of the N2 peak amplitudes showed significantly larger amplitudes for the forward motion conditions than for the backwards motion conditions, indicating an activation of a larger pool of neurons for forwards motion, or an increased sensitivity for forwards motion.

The time-frequency analysis showed a desynchronization in the alpha frequency band in channel PM in response to all motion conditions. This was thought to reflect the processing of visual information, or a heightened attentive or anticipatory state. The alpha band synchronizations found in the static conditions was interpreted as the brain being in an idling or resting state. A significant desynchronization in the beta frequency band was also found, thought to reflect communication between brain hemispheres. These results taken together could imply that the speed at which we process information regarding ego-motion is greatly influenced by the velocity of our movement through the environment, and not so much by whether the movement is forwards or backwards.

1.0 **Introduction**

The concept of optic flow was first introduced by James Gibson. It describes the way in which structured light reflecting off textures, objects and surfaces gives organisms vital visual information as they move through their environment (Gibson, 1966). Together these make up what is referred to as the optic array and by means of invariants in the environment an organism's motion provides it with a constantly changing sample of the optic array which transforms smoothly (Golonka & Wilson, 2012). Invariants are the unchanging physical properties of the environment.

Among other things, the continuously changing optic array provides information about direction of heading and the three-dimensional structure of the environment (Morrone et al., 2000). It can be defined as the flow of changes in the optic array caused by the relative motion between an organism and its environment (Golonka & Wilson, 2012).

An important part of Gibson's theory is the focus of expansion. This is the point from which the visual information in the optic array flows. In other words, the focus of expansion will be in the direction you are heading (Gibson, 1966).

Several researchers have studied the concept of optic flow. Findings indicate that it is used as a source of information regarding heading (Van Den Berg, 1992), locomotor control (Warren et al., 2001), postural sway response (Musolino, Loughlin, Sparto & Redfern, 2006) and obstacle avoidance (Menuchi & Gobbi, 2012). Optic flow can thus be seen as an essential part of visual information necessary to navigate through our environment in a safe and deliberate way. Despite knowing this, several questions still remain unanswered. One question that needs answering is: How do we process differences in velocity and direction in the changing optic array during ego-motion?

The flow of visual information from the environment can either expand or contract on the retina depending on the direction in which a person is moving. After the light signals are picked up by photoreceptor cells in the retina, visual information is sent to the striate cortex, also known as visual cortex (V1) (Zeki et al., 1991). There are different pathways of visual information processing in the brain that differ in function. The magnocellular pathway is thought to be mainly responsible for visual information regarding motion. The parvocellular pathway, on the other hand, is thought to be designated to visual information regarding colour

(Zeki et al., 1991). The magnocellular pathway terminates in layer 4Cα of the striate cortex (V1), while the parvocellular pathway terminates in layer 4Cβ. V1 information from the parvocellular pathway continues on to what is known as the ventral stream. The ventral stream goes from V1 to V2, then on to V4 before terminating in the temporal lobe. Information from the magnocellular pathway continues through what is known as the dorsal stream. The dorsal stream goes from V1 to V2, then goes on to the MT+ complex, before terminating in higher areas of the parietal and temporal lobes (Purves et al., 2012; Liu & Newsome, 2002). The dorsal stream is where motion stimuli are thought to be processed including information about complex optic flow patterns (Jokisch, Daum, Suchan &Troje, 2005).

There has been extensive research regarding how the brain processes motion information, and exactly which part of the brain is responsible for this. Research on macaque monkeys and human beings has implied the MT+ complex (V5) to be the part of the brain mainly designated to motion processing (Probst, Plendl, Paulus, Wist & Scherg, 1993; Zeki et al., 1991). The MT+ complex incorporates the MT (medial temporal) and MST (medial superior temporal) regions. The complex motions in optic flow, such as expansion, contraction and rotation, are thought to be encoded in area MST and these visual patterns occur during self motion through the environment (Wunderlich et al., 2002). Several other studies have also implied the MST in the processing of optic flow (Van der Meer, Fallet & Van der Weel, 2008; Probst et al., 1993). In an fMRI study by Smith, Wall, Willliams & Singh (2006) it was found that the human MST is activated the strongest by complex flow that contains multiple components such as expansion, contraction and rotation. Area MT was, on the other hand, activated equally, both by random motion and other moving dot patterns, indicating that there may be a specialization for the processing of optic flow information in area MST. This result was corroborated by Ptito, Kupers, Faubert and Gjedde (2001) who found that area MT in humans was not involved in the processing of optic flow information but rather higher parietal areas that are predominantly in the right hemisphere.

When researching the processing of motion speed in the MT+ complex, it has been found that it contains different neurons tuned to different speeds of motion (Liu & Newsome, 2003). Areas MT/V5 and MST have also been shown to be sensitive to speed gradients that are an important cue for extracting depth structure from the optic array when perceiving the

three-dimensional layout of the visual environment (Orban, 2012; Duffy & Wurtz, 1997). There can be either a positive speed gradient where the speed increases from the point of fixation and outwards, or a negative speed gradient where the speed increases from the periphery and inwards to the point of fixation.

Although the MT+ complex has been implicated by several researchers in the processing of optic flow, the question of what actually occurs in this part of the cortex when perceiving motion is not yet fully understood. A tool that has been utilized by several researchers to gain more knowledge regarding this is the electroencephalogram (EEG), and the study of visual evoked potentials (VEP) (Van der Meer, Fallet & Van der Weel, 2008; Kuba & Kubova, 1992).

After a visual stimulus has been presented an electrical potential both time- and phase-locked to the stimulus can be observed in the cortex, hence the term visual evoked potentials (Pfurtscheller & Lopes da Silva, 1999; Smith, Wall, Lingnau & Ashida, 2006). This fact makes it possible to use averaging techniques to enhance the signal-to-noise ratio, making the evoked activity clear.

In general, evoked potentials are thought to reflect underlying components connected to different brain activities and the processing of different stimuli (Handy, 2005). A component can be defined as a scalp-recorded neural activity that is generated in a given neuroanatomical module when a specific computational operation is performed (Handy, 2005). Several different components have been identified in response to different stimuli, but one VEP component that has been found to have a connection to the processing of motion is the N2, or N200 component (Heinrich, 2007; Kuba & Kubova 1992; Jokisch et al., 2005).

The N2 component is the second negative peak on the VEP waveform (Smith, Wall, Lingnau & Ashida, 2006), and usually has a latency between 130-250 ms (van der Meer et al., 2008). This N2 component can be influenced by different aspects of the stimuli, and findings indicate that the latencies of the N2 component decrease as the velocity of a motion stimulus increases (Heinrich, Van der Smagt, Bach & Hoffman, 2004).

However in an unpublished Master's thesis, Vilhelmsen (2013) reported that when using an optic flow stimulus, the N2 latencies increased as the speed of the stimulus increased. Several researchers have used simpler stimuli like moving dot patterns in their research, as was done in a study by Maruyama, Kaneoke, Watanabe and Kakigi (2002). They found that when using a random dot kinematograph (RDK), the latencies decreased as the stimulus speed increased. These differences may be attributed to the stimulus that was utilized. In the study performed by Vilhelmsen (2013), an ecologically valid optic flow stimulus designed to simulate ego-motion was used, as is the case in the present study. A magnetoencephalographic study by Bakardjian, Uchida, Endo & Takeda corroborated the findings of Vilhelmsen (2013), and found greater latencies with increased velocities of apparent motion created by moving bars.

The amplitude of the N2 component has also been found to vary depending on different factors such as velocity (Muller, Göpfert, Breuer & Greenlee, 1999), motion adaptation (Hoffman, Dorn & Bach, 1999; Bach & Ullrich, 1994), and contrast and luminance of the stimulus (Kuba & Kubova 1992).

In addition to information about the evoked potentials, EEG data also contain information about induced oscillatory activity (Pfurtscheller & Lopes da Silva, 1999). This oscillatory activity is sometimes referred to as induced or non-phase locked activities. Compared to the visually evoked potentials which are both phase- and time-locked to the stimulus, the induced oscillatory activity is time-locked but not phase-locked to the stimulus (Bastiaansen, Mazaheri & Jensen, 2012). There will always be oscillatory activity, and event related oscillatory activity can be regarded as modulations of this. The induced oscillatory activity can be analyzed by means of a time-frequency analysis in which one can see the induced changes in amplitude resulting from an increase or decrease in neuronal synchrony from a baseline to a specific time-frequency point when comparing two conditions (Van der Meer et al., 2008; Pfurtscheller & Lopes da Silva, 1999). When this analysis is performed, either synchronized or desynchronized oscillatory activity can be seen in different frequency bands.

One frequency band that has been implied by several researchers in connection to the processing of visual stimuli is the alpha frequency, where findings indicate that a visual

stimulus causes an event related desynchronization (ERD) in the occipital region of the cortex (Pfurtscheller, Neuper & Mohl, 1994; Clapp, Muthukumaraswamy, Hamm, Teyler & Kirk, 2006). The ERD in the alpha band does, however, not just occur when subjects are processing information regarding visual stimuli, but also when they are in an attentive state, anticipating visual stimuli or during the execution of a motor command (Onoda et al., 2007). Localized desynchronization in the alpha frequency band can thus be interpreted to denote a cortical area in which excitability has increased.

In addition to desynchronized activity in the alpha frequency band, synchronized alpha activity can also be observed. It occurs in a cortical area of at least a few cm^2 which is not processing information nor is it ready for processing information, and some refer to this state as cortical idling (Pfurtscheller, Stancák & Neuper, 1996). Thus, a cortical area of at least some cm^2 in which synchronized alpha activity can be observed can be interpreted to denote an area in which cortical excitability has decreased. In addition to being implied in the maintenance of attention, Klimesch (1999) found evidence for the possible role of alpha band frequency oscillatory activity in relation to cognitive and memory performance.

There is not only a division between the beta, alpha, theta and delta frequency bands. The alpha-band ERD can further be divided into the upper (10-12 Hz) and lower alpha band (7-10 Hz) (Pfurtscheller & Lopes da Silva, 1999). According to Pfurtscheller et al. (1994) the upper alpha-band ERD is more focused over occipital areas, has a shorter duration than the lower alpha-band, and is more spatially restricted. The upper alpha-band is also more task-specific and may reflect computational processes such as feature extraction, stimulus identification and response preparation in a movement task. The lower alpha band, on the other hand, is relatively widespread with a maximum over parietal areas, and can be thought of as reflecting task-independent processes related to cognitive processing (Pfurtscheller et al., 1994; Pfurtscheller, 1992).

What has become apparent to researchers working with induced oscillatory activities is that individual cortical areas seem to be part of more than one functional network (Pfurtscheller et al., 1996). This means that a cortical area can serve more than one function depending on which network it is currently coupled to. One proposed function of the synchronized and desynchronized activity is the coupling and uncoupling of these functional networks, and cortical areas which are part of the same functional network are thought to be

identifiable by the frequency of their oscillatory activity (Bastiaansen, Mazaheri & Jensen, 2012). According to Pfurtscheller et al. (1996), the size and magnitude of ERD also reflects the mass of neural networks involved in the performance of a specific task at a moment in time.

A theory as to what the cause of the synchronized and desynchronized oscillatory activity may be has implied the thalamus. Lopes da Silva (1991) is one of the proponents of this theory, in which the thalamus is responsible for the generation of both synchronized and desynchronized oscillatory activity by either blocking or relaying sensory information from the thalamic nuclei to the cortex. When sensory information is inhibited, synchronized alpha activity will occur. In the opposite case, if the sensory information is relayed from the thalamus to the cortex, blocking of the occipital alpha rhythm occurs and one will see desynchronized activity (Lopes da Silva, 1991). This thalamo-cortical gatekeeping and suppression of alpha activity has also been proposed to play a part in attentionally mediated selective suppression of distracting information (Foxe & Snyder, 2011; Mathewson et al., 2011).

In the current study we investigated the way in which the brain interprets different speeds of simulated motion, both forward and backward. Using high-density EEG, differences in both the induced and the evoked activity of the brain as a function of the exposure to different speeds and directions of simulated ego-motion were investigated.

Research has been carried out on this subject before by Vilhelmsen (2013). However, in that study the stimulus conditions were three different speeds of simulated forwards ego-motion. In the present study, two speeds of both forwards and backwards motion were incorporated. Based on the findings of Vilhelmsen (2013), it was expected that there would be an increase in the N2 peak latencies, and a decrease in amplitudes with increased stimulus speed. It was not clear whether the latencies would be significantly different as a result of the motion direction. It was, however, expected that amplitudes would be higher for the forward motion conditions than for the backwards motion conditions, based on findings that indicate a greater activation for expansion when compared to contraction (Holliday & Meese, 2005; Maloney, Watson & Clifford, 2013).

Thus the goal of the current study was to investigate if there were any differences in the N2 peak latencies between the different speeds of simulated forwards and backwards ego-motion, and to further investigate what changes in induced oscillatory activity occur as a result of optic flow.

2.0 Method

2.1 Participants

A total of 17 participants were recruited from Dragvoll campus, NTNU. The age span was from 20 to 28 years old (mean = 24 years, SD=2.35). The participants were asked if they were right or left handed. One of the participants was left-handed, the rest were right handed. Data from four of the participants had to be discarded due to noise interference, leaving data from 13 participants (7 males) for further analysis. Participants gave their informed consent, and were at liberty to withdraw from the experiment at any given time. The Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences approved the study.

2.2 Stimuli

Stimuli consisted of poles on each side of a road moving forward and backward at two different speeds (see Figure 1). This was projected onto a screen (1.08 m x 0.705 m) by an ASK M2 projector with a refresh rate of 60 Hz, and a resolution of 593 pixels per meter. The stimulus was generated using E-Prime software. The participants were seated approximately 75 cm from the screen.
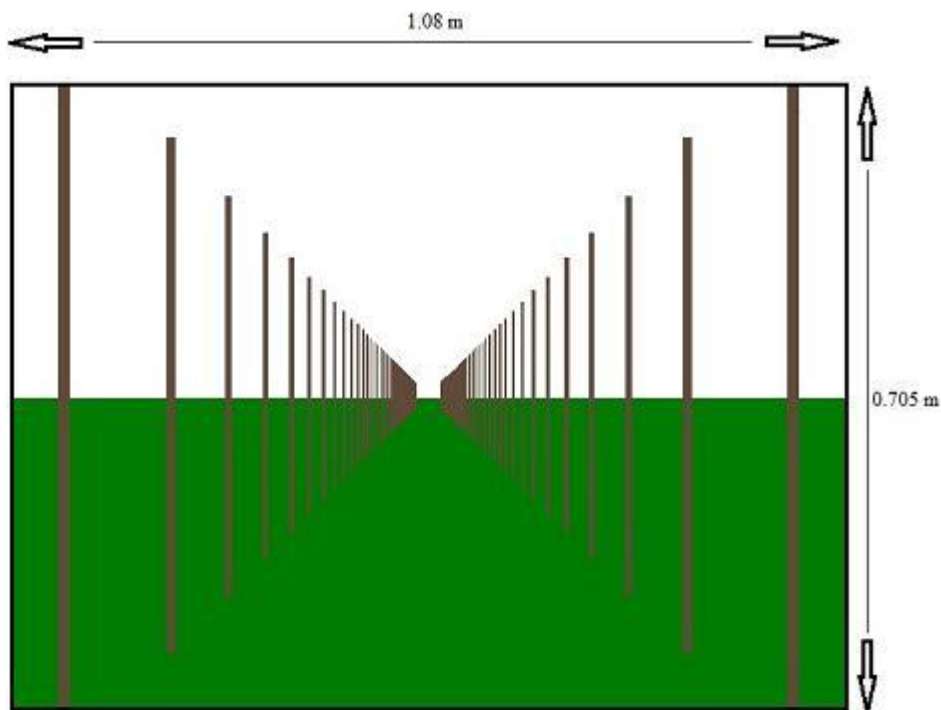
Figure 1 *Screen shot of the optic flow stimulus. The poles moved either from the centre towards the edges of the screen, or from the edges towards the centre of the screen simulating forwards and backwards ego-motion at two different velocities.*

Both forwards and backwards motion had two speeds, either high (50 km/h) or low (17 km/h). The stimuli consisted of poles placed alongside a road, and in the forwards condition poles started out from the center centre of the screen and moved outwards until they left the screen. In the backwards motion condition poles entered from the edges of the screen and moved towards the center. There was also a static control condition in between motion conditions in

order to prevent motion adaptation. The number of poles was the same in this static condition as in the preceding trial, to avoid a difference in luminance between the motion and static conditions (Vilhelmsen, 2013). The length of the road was 30 meters and the length of the stimulus was 1500 ms, both in the motion and static conditions. There were 75 trials for each of the four motion conditions, and 300 trials for the static control condition.

2.3 Apparatus

The equipment used to record EEG activity was the Geodesic Sensor Net 200 (GSN), with 256 electrodes (Tucker, 1993). The net was connected to an amplifier, and the impedance of the electrodes was kept under 50 kΩ to ensure an optimal signal-to-noise ratio (Ferree, Luu, Russell & Tucker, 2001). 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.
The EEG signals where amplified and sent to a Macintosh computer where they were saved for offline analysis. A digital camera recorded the participants' behaviour during the trials.

2.4 Procedure

The circumference of the participant's head was first measured to select the appropriate net (small, medium or large). The net was soaked in a saline electrolyte for 15 minutes. The net was then fitted on the participant's head, before the participant was led into the experimental room. A sound-proof glass window separated the experimental room from the control room where assistants operated the computers used for data acquisition. The participant was seated in a chair in front of the wide screen and the net was plugged into the amplifier. The participant was then told to focus their attention to the middle of the screen. Impedance was checked and if necessary, electrode contact was improved by adding saline electrolyte or adjusting the positions of the electrodes. The experiment lasted about 15 minutes.

2.5 Analysis

Brain data analysis

BESA software version 5.3 was utilized to analyse the data. Averaging epoch was set from -500 to 1000 ms. Low cut-off was set to 1.6 Hz to remove slow drifts in frequencies, and high

cut-off was set to 60 Hz. Bad channels were removed, but no more than 10% (24 channels). Epochs in which there were artifacts from eye blinks, head movement and facial muscle activities were also removed. Threshold values for gradient and low signal were set at 75µV and 0.1 µV, respectively, and maximum amplitude was at 200 µV.

Out of 75 presented trials for each motion condition the average trial contribution for all participants were 73 (SD= 1.3) for low forwards speed, 73 (SD= 1.1) for low backwards speed, 73 (SD= 1.2) for high forwards speed, 73 (SD= 1.1) for high backwards speed and (out of 300) 290 (SD= 2.9) for the static control condition.

VEP analysis

Each participant's data were averaged and these averages were re-referenced to an artificial reference calculated from the average potentials over the scalp, and interpolated to 81 standard electrode positions (Van der Meer et al., 2008). The individual averages were then combined into a grand average. This grand average was examined manually, and the four posterior electrodes with the largest amplitudes on the N2 peak in the low forwards condition were selected. During this examination, low cut-off was set to 1.6 Hz to remove slow drift in the data, high cut-off was set to 30 Hz and the notch filter was set to 50 Hz.

The electrodes chosen were posterior electrodes P4, PO4, POz and P2. These electrodes were chosen based on the fact that they exhibited the highest amplitude on the N2 peak. The amplitude is thought to reflect the number of synchronously activated neurons (Pfurtscheller & Lopes da Silva, 1999), and this can thus be interpreted to reflect an area in which more neurons are sensitive to the optic flow stimulus presented. Further, these four electrodes where located in the parieto-occipital area where optic flow activity is expected to be processed.

N2 peak latency and amplitude values from these four electrodes were then analysed in SPSS (IBM SPSS Statistics 19). Two separate two-way repeated measures ANOVAs were conducted. One to check for significant differences in N2 latency between the two speeds of forwards and backwards motion (low forward, low backward, high forward and high backward) in channels P4, PO4, POz and P2. The other was used to check for significant differences in N2 peak amplitude in the same channels.

Time-frequency analysis

In addition to an analysis of the VEP components, a time-frequency analysis was carried out in BESA 5.3. A 4-shell ellipsoidal head model (Berg & Scherg, 1994; Hoechstetter, 2004) was applied to the EEG data and the ongoing EEG was transformed into source montage dipoles. This allowed each equivalent dipole to image the source currents in the surrounding tissues that are parallel to the dipole's orientation (Probst et al., 1993). The sources were (with Talairach (Talaraich & Tournoux, 1988) coordinates: 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.

Frequency and time samples were set to 1 Hz and 50 ms. Low cut-off was set to 4 Hz, while high cut-off was set to 35 Hz. Evoked activity was removed before computing a TSE, and power (μV^2) was used to measure the induced activity. For the time-frequency analysis the epoch was set to -500 to 1000 ms.

Paired samples t-tests were conducted in BESA Statistics 1.0 to test for significant differences between conditions in the time-frequency domain. TSE data from all participants were averaged and analysed together. To avoid obtaining a significant result by chance after doing several t-tests, permutation in combination with data clustering was utilized. This meant that the data from each of the conditions were interchanged a set number of times, dependent on the number of conditions and subjects. Initial t-tests were performed, which yielded a number of data clusters in which a significant effect was found. These were then put through permutations, and new t-tests for significant clusters were performed. By using the distribution of all of the clusters from each of the permutations, the significance of the initial significant clusters was assessed. There were 8192 permutations for each t-test, and frequency ranges and epochs were the same as in the time-frequency analysis.

3.0 Results

3.1 VEP analysis
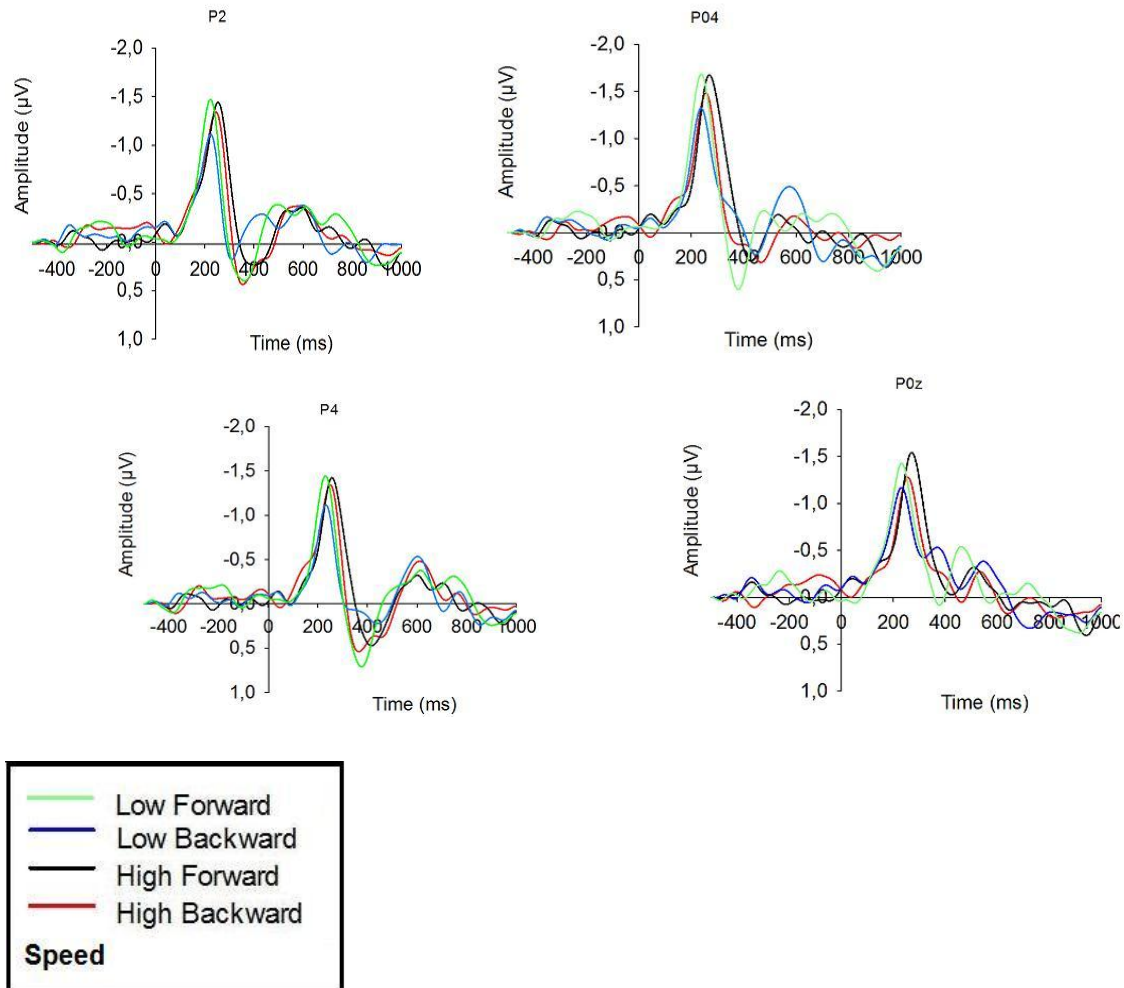
Figure 2 *Grand average motion VEP's for posterior electrodes P4, PO4, POz and P2. The low speed forwards waveform is shown in green, the low speed backwards waveform in blue, the high speed forwards waveform in black and the high speed backwards waveform in red.*

Repeated-measures ANOVA's were performed for latency and amplitudes with speed (high and low) and direction (forward and backward) as within-subjects factors. The electrode chosen for the analysis was the one with the highest amplitude in the low speed forwards condition and was always one of the posterior electrodes P4, P04, P0Z or P2. The electrode chosen varied among the participants, but once we had chosen one for a given participant this was used in all of the four motion conditions.

The mean N2 peak latency was 245 ms for the low speed forwards condition (SD =

39), 242 ms for the low speed backwards condition (SD = 35), 264 ms for the high speed forwards condition (SD = 31) and 259 ms for the high speed backwards condition (SD = 30) (see Figure 3).
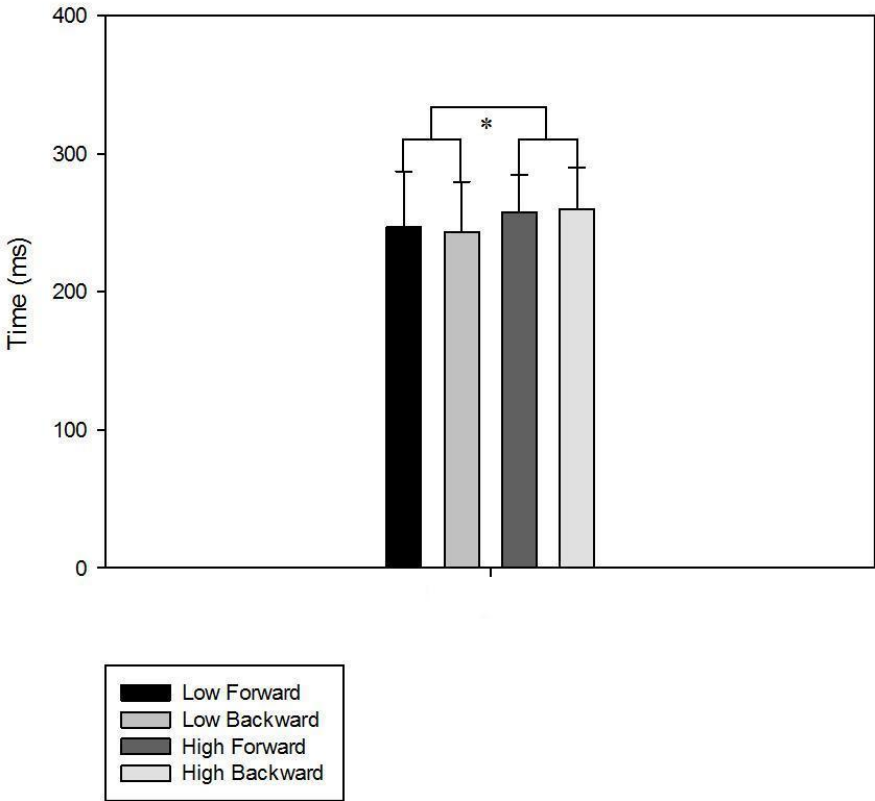
Figure 3 *Group mean peak latencies (and SDs) for low speed forward motion, low speed backward motion, high speed forward motion and high speed backward motion.* * Significant at the p < 0.05 level.

The ANOVA measuring the effect of stimulus on latency revealed a significant effect of speed on latency, $F(1,12) = 6.2$, p < 0.05. This indicates that the N2 peak latencies in the low speed conditions were significantly lower than in the high speed conditions. There was no significant effect of motion direction on the N2 peak latencies, nor was there an interaction effect.

The mean N2 peak for the amplitudes was -2.71 for low forwards (SD=1.95), 2.02 for low backwards (SD=2.03), -2.76 for high forwards (SD=2.39) and 2.49 for high backwards (SD=2.33) (see Figure 4).

The ANOVA measuring the effect of stimulus on amplitude revealed a significant effect of motion direction, $F(1,12) = 5.8$ $p< 0.05$. This indicates that backwards motion resulted in significantly smaller amplitudes than forwards motion. There was no significant effect of speed on the N2 peak amplitudes, nor was there an interaction effect.

Amplitude (µV)

	Low Forward
	Low Backward
	High Forward
	High Backward
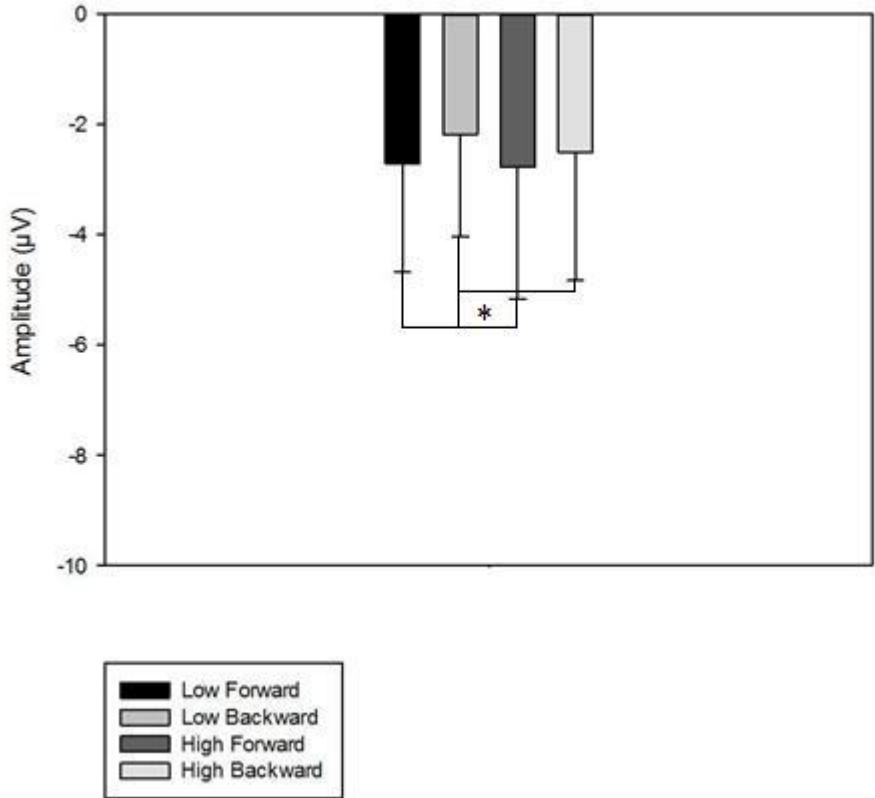
Figure 4 *Mean N2 amplitudes for conditions low forward, low backward, high forward and high backward.* Significant at the p < 0.05 level.

3.2 Time-frequency analysis

A time-frequency analysis was carried out for two speeds forwards, two speeds backwards and a static control condition for all participants. The four conditions: low speed forwards, low speed backwards, high speed forwards and high speed backwards were each compared to the static control condition. Participants showed induced desynchronization in the alpha frequency band at about 300 ms after stimulus onset to the end of the stimulus in all four motion conditions. Significant desynchronization in the beta frequency band was also found. There was however some individual differences, and not all participants showed this pattern of desynchronized activity. A TSE for a typical participant can be seen in Figure 5.

Figure 5 *TSE map of the low speed forwards condition (left) and the static condition (right) for a typical participant (Subject I), in source PM. The red vertical line at t=0 ms indicates stimulus onset.*
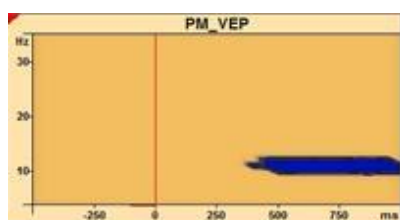
Figure 6 *TSE probability map (p<0.05) for a typical subject (Subject I) in the forwards low speed condition. The red vertical line indicates stimulus onset.*

The averaged TSE data from all the participants were compared to the static control condition. This was done for each of the four motion conditions. The averaged TSE data from a motion condition were also compared to the other motion conditions. The maximum activity was found in the alpha band (9-11 Hz), in the time range from 300 – 800 ms. TSE plots of averaged data from all participants for source PM in the high speed forwards and static condition can be seen in Figure 7. Here, oscillatory activity in the high speed forwards motion condition can clearly be seen to be different from that in the static condition. The motion condition shows desynchronized activity in the alpha frequency band, while the static condition shows synchronized activity. A comparison of the high speed forwards condition and static condition can be seen in Figure 8. No significant differences were found when each motion condition was compared with the other.
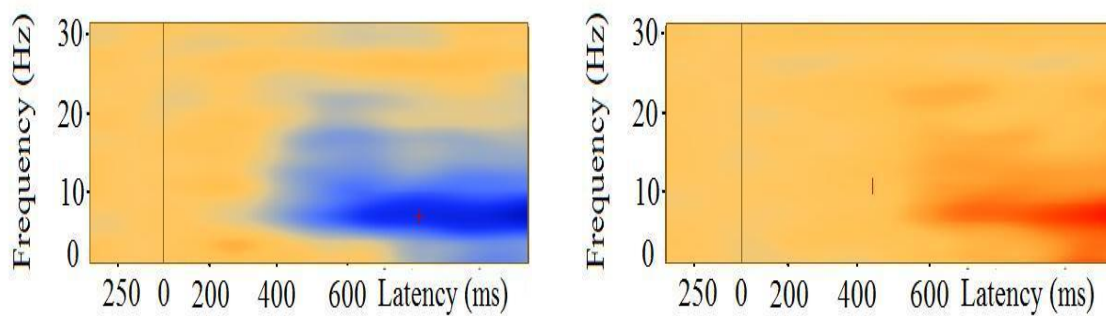
Figure 7 *Averaged TSE plots for all the participants in the PM source. To the left is the high speed forward condition and to the right is the static control condition. In the high speed forwards condition areas of desynchronized activity can be observed (blue).In the static condition areas of synchronized activity can be observed (red).*
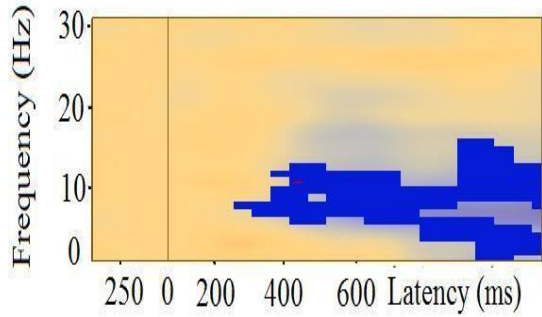
Figure 8 *TSE statistics plot of source PM. The cluster values from the static condition have been subtracted from the cluster values of the high speed forward condition. The blue area in this plot indicates that there is a significant (p<0.05) negative difference between these cluster values, indicating an induced de-synchronization in the alpha frequency band.*

In addition to desynchronization in the alpha frequency band, significant desynchronized activity in the beta frequency band was observed (see figure 9)
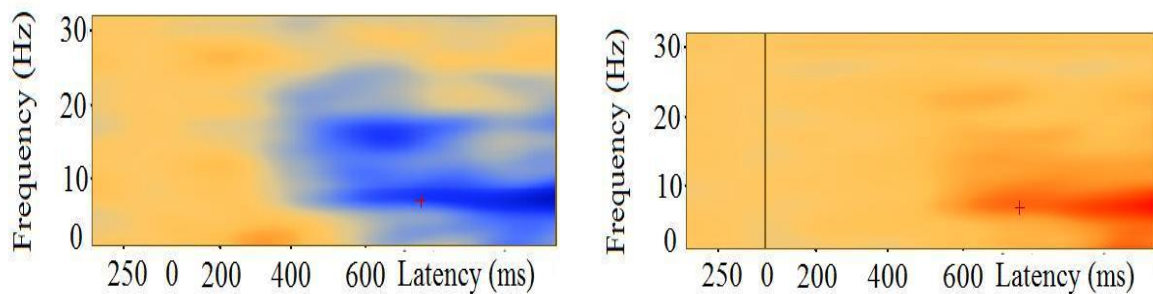
 Figure 9 *Averaged TSE plots for all the participants in the PM source. To the left is the low speed backward condition and to the right is the static control condition. In the low speed backward condition areas of desynchronized activity can be observed (blue).In the static condition areas of synchronized activity can be observed (red).*
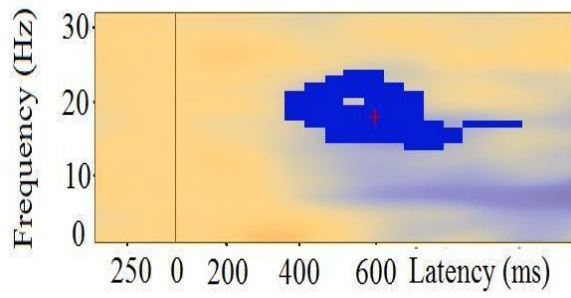
Figure 10 *TSE statistics plot of source PM. The cluster values from the static condition have been subtracted from the cluster values of the low speed backward condition. The blue area in this plot indicates that there is a significant (p<0.05) negative difference between these cluster values, indicating an induced de-synchronization in the beta frequency band.*

4.0 Discussion

In this study, high-density EEG was used to measure the electrical brain activity caused by an optic flow stimulus at two different speeds, both forward and backward. Scalp potentials in channels P4, P04, P0Z and P2 were investigated for the different conditions.

Significant differences in N2 peak latencies were found between the low speed motion conditions and the high speed motion conditions, indicating that the N2 peak latencies in the low speed conditions were significantly lower than in the high speed conditions. There were however no significant differences between the N2 peak latencies of the forward and backward motion conditions. The analysis of N2 peak amplitudes showed significant differences between the forwards and backwards motion conditions, indicating larger amplitudes for the forward motion conditions. No significant difference in amplitude was found between the high and low speed conditions.

The time-frequency analysis showed a desynchronization in the alpha frequency band in response to all motion conditions. This pattern of desynchronized alpha frequency band activity was found in the PM source.

This study showed a significant effect of motion speed on latency, and the latencies were seen to increase as the speed of the stimulus increased. The fact that the latencies of the N2 component can be influenced by different factors, one of these being the velocity of the stimulus has been documented before (Maruyama, Kaneoke, Watanabe & Kakigi, 2002). However Heinrich et al. (2007) stated that the usual finding is a decrease in N2 peak latencies as the velocity of the stimulus increases. The findings in the present study however indicate the opposite.

It is important to note that although an increase in latency is what is usually found, there have also been other studies that have shown results similar to those of the current study. A magnetoencephalographic study by Bakardjian, Uchida, Endo & Takeda (2002) found greater latencies with increased velocities of apparent motion created by a moving bar stimulus. Kawakami et al. (2002) also found an increase in latencies with increased velocities, but their study used a non-gradient stimulus lacking perspective which makes it less suited for a direct comparison. After all, speed gradients are an important cue for extracting depth structure (Orban, 2011; Duffy & Wurtz, 1997). A better comparison would be the unpublished master thesis by Vilhelmsen (2013), where the latencies were seen to increase as

a result of increased stimulus speeds. The stimulus used in that study to simulate ego-motion was similar to that of the current study. Given that both of these studies found increasing latencies with increasing velocities, it may be an indication that the differences in latencies could be related to the stimulus. In other optic flow research, a dot or checkerboard stimulus is often utilized (Van der Meer, Fallet & Van der Weel, 2008; Probst et al., 1993). As previously mentioned, a component can be defined as the scalp recorded neural activity generated in a given neuroanatomical module when a specific computational operation is performed (Handy, 2011). The results from the current study could then imply that the optic flow pattern that was used is more complex, or closer to actual ego-motion, than dots or checkerboard stimuli and thus takes longer to process with higher velocities, resulting in an increase in the N2 peak latencies. Since the same pattern of increase in latencies was also found by Vilhelmsen (2013) during his study with the same stimuli, this seems a plausible explanation.

This also means that in the current study the variable that is implied to have a significant effect on the N2 peak latencies is the speed of the stimulus, not its perceived direction. This indicates that information regarding motion both forwards and backwards is processed in about the same time, and may also be processed in the same area of the cortex. Thus, these results can be interpreted to mean that moving through our environment at a high speed takes longer for our brain to process than if we were to move through it at a lower speed, but whether the direction is forwards or backwards is less important (Vilhelmsen, 2013; Bakardjian, Uchida, Endo & Takeda, 2002).

This study showed a significant main effect of motion direction on amplitude. When investigating the amplitudes for the different conditions, it becomes apparent that the highest amplitudes occur in the forwards conditions. The amplitudes in both of the forwards motion conditions were found to be significantly higher than those of the two backwards motion conditions.

In a previous MEG study by Holliday and Meese (2005), it was shown that the evoked magnetic response was greater for expansion than for other complex motions such as contraction and rotation in the MT+ area. This was thought to indicate the activation of a larger pool of neurons to expansion. According to Pfurtscheller and Lopes Da Silva (1999), amplitude can be seen as an indication of the number of neurons synchronously activated. Thus, the present results might imply that the two conditions of forwards motion activate a larger number of neurons tuned for expansion, which in turn results in the larger amplitudes

observed. One way to interpret this is that there is an increased sensitivity to forwards motion compared to backwards motion. The implication that we seem to have more neurons tuned to forwards motion is not surprising, as people spend most of their lives moving more forwards than backwards.

In addition to an analysis of the VEP's, a time-frequency analysis was performed to inspect the induced oscillatory activity caused by the four different conditions of stimulus motion. Significant desynchronization in the alpha and beta frequency band was observed in the PM source in most participants, but not all. These individual differences may be caused by the 4-shell ellipsoidal head model that was used as sources for the TSE, which is an average based on MRI data from normal adults (Berg & Scherg, 1994). Individual brain variations from this average could be a reason why the equivalent dipoles were not able to image the source currents with precision in some of the participants. It is also important to note that the desynchronized alpha activity was not only observed in the PM source, but this was however the source in which the most activity was seen.

The desynchronization of oscillatory activity in the alpha band can be seen as a result of a heightened attentive state, anticipation of visual stimuli, during the execution of a motor command or during the processing of visual information (Pfurtscheller et al., 1994; Clapp et al., 2006; Onoda et al., 2007). When studying the TSE for the static conditions, synchronized oscillatory activity in the alpha frequency band can be seen. Synchronized oscillatory activity in the alpha frequency band is sometimes referred to as a state of cortical idling (Pfurtscheller et al., 1996). It implies that a certain part of the cortex is either not prepared for nor in the middle of processing information. However, a short time after stimulus onset the TSE shows a marked desynchronization in the alpha frequency band in the PM channel. This is thought to indicate increased cortical excitability, meaning that this part of the cortex is either prepared for, or in the middle of processing information. We see then a shift in these three sources from a resting to an active state, as a result of the presentation of the moving visual stimulus.

The alpha frequency band can be further divided into the upper and the lower alpha, with the lower being more widespread, the upper being more spatially restricted and task specific (Pfurtscheller et al.,1994). Because the data were not clear-cut and there was a certain degree of variation between participants, it was not possible to determine whether the alpha activity in participants was in the upper or lower alpha band. Because of this it is difficult to conclude that the alpha activity we were observing was caused by the processing

of visual stimuli based on the TSE analysis alone. Alpha frequency desynchronization can also be seen when one is in a heightened attentive or anticipatory state (Onoda et. al, 2007). Given that the participants had to focus and pay attention to the stimulus presented and were expecting it to change, part of the desynchronized activity could indeed be attributed to an increased need for attention, or the anticipation of the stimulus. However, when we take into account the N2 components found in the VEP analysis, and the fact that the changes in oscillatory activity occurred in a source in the MT+ region, it seems plausible that the induced activity is a result of the optic flow stimuli. The desynchronized activity also seems to occur a certain time after stimulus onset, after about 300 ms, indicating that the activity is a direct response to the stimulus. A possible explanation for the observed desynchronized activity could then be the processing of optic flow, which would concur with previous findings of an induced desynchronization in the alpha frequency band in parieto-occipital areas following visual stimuli (Neuper & Pfurtscheller 2001; Clapp et al., 2006).

Significant desynchronized beta activity was also observed. This activity has been theorized to facilitate communication between brain hemispheres, which is thought to play a part in the integration of moving elements into global object motion (Lorenceau, Aissani, Martinerie, Cherif & Paradis, 2014). In other words, both desynchronized alpha and beta activity is connected to the processing of ego-motion.

In addition to comparing the four motion conditions to a static condition, they were also compared to each other, and no significant differences were found. This means that all four motion conditions resulted in the same desynchronization in the alpha frequency band. These findings imply that visual information regarding motion is processed in the same place, irrespective of speed or direction.

In conclusion, significant differences were found in N2 peak latencies of participants exposed to different conditions of simulated ego-motion. The lower latencies of the low speed conditions can be interpreted as an increase in complexity which led to an increase in the time it took to process the stimulus, which resulted in the longer latencies.

Significant differences were found in N2 peak amplitudes, with the forward conditions having the highest amplitudes. These differences were interpreted to be a result of the number of neurons synchronously activated during forwards and backwards motion.

The induced oscillatory activity for the motion conditions revealed a desynchronization in the alpha frequency band in the PM source. There was a difference in the oscillatory activity in

the motion and static conditions, but not between the motion conditions. This was thought to reflect the processing of visual information, or a heightened attentive or anticipatory state. The alpha band synchronizations found in the static conditions were interpreted as the brain being in an idling or resting state. A significant desynchronization in the beta frequency band was also found, thought to reflect communication between brain hemispheres

These results could then imply that whether a person moves through the environment backwards or forwards will be processed in much the same way. What makes a difference in the time it takes to process perceived ego-motion might in fact be the speed at which the person moves. A possible way forward could then be to explore this further, perhaps by excluding backward motion as a variable and adding a wider range of speed conditions.

5.0 References

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Appendix A

TSE plots from all participants A-M in the low forward, low backward, high forward, high backward and static condition. Blue areas indicate a decrease in induced oscillatory activity (de-synchronizations) while the red areas show an increase in induced oscillatory activity (synchronizations). Epochs are set from -500 to 1000 ms, range 2 – 30 Hz, and the measure unit was power (µV2.) Alpha de-synchronization can be seen in source PM, but also other sources. Sources used are: from top left to bottom right): VClL, PM, VClR, VCrL,VCvM, and VCrR. Red line indicates stimulus onset.

Low Forward

A
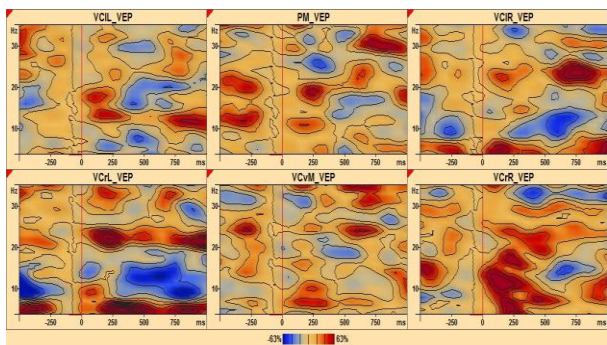
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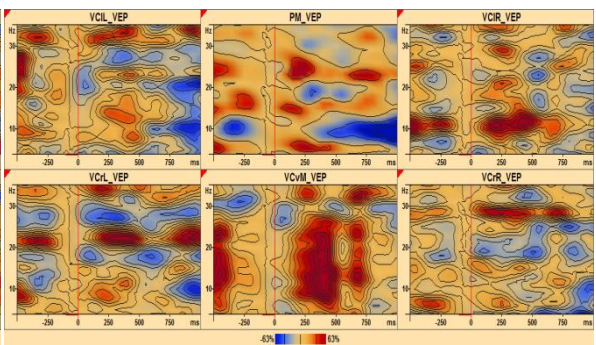
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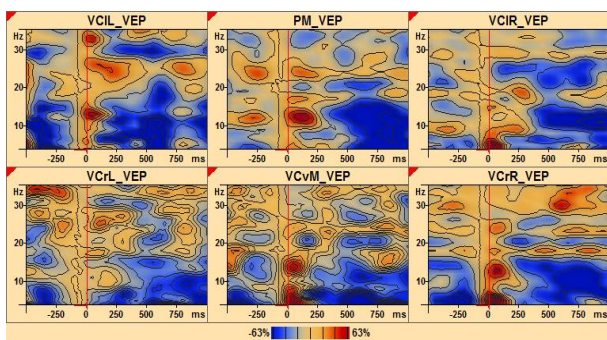
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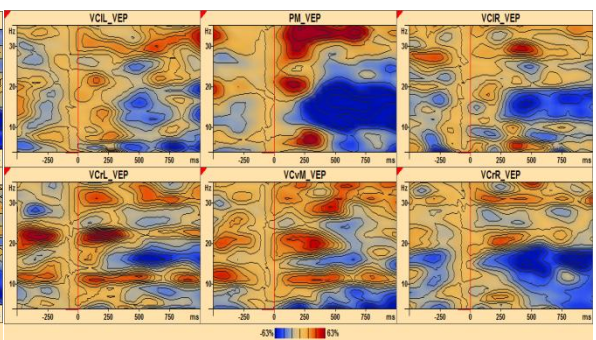
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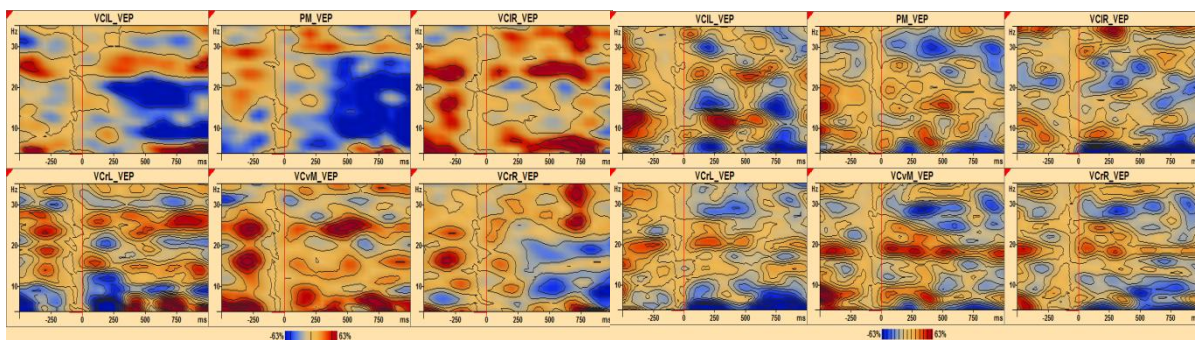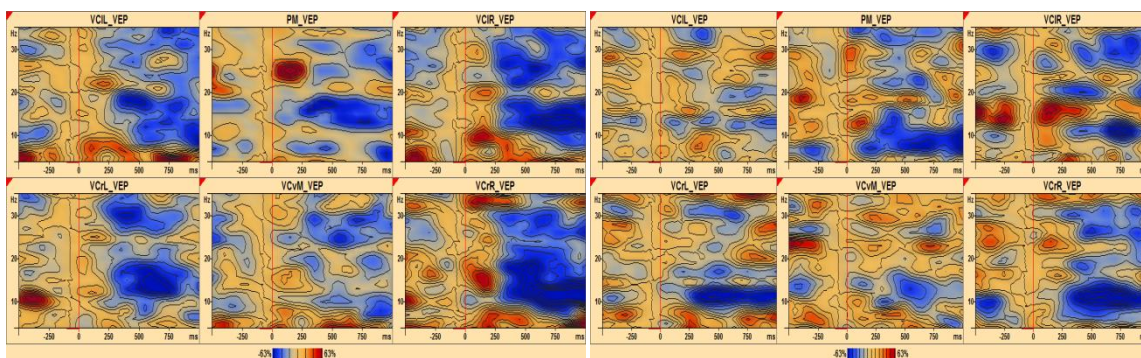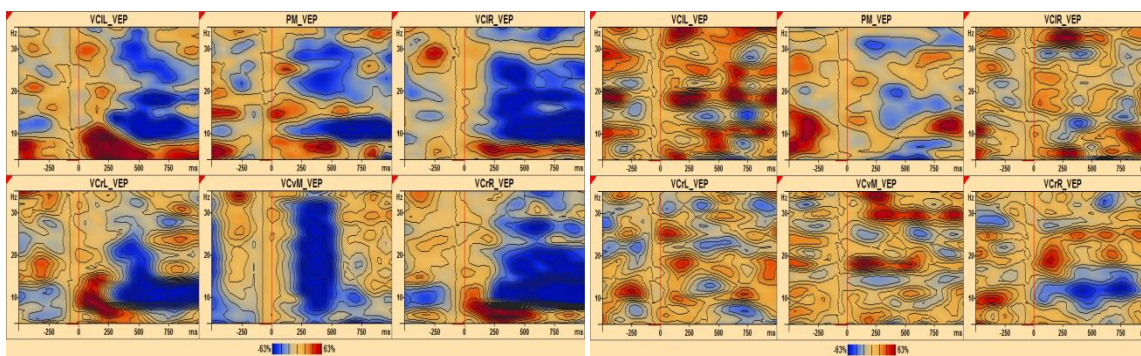
F

G

H

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K

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Low Backward

A

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C

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High Forward

A

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L

M
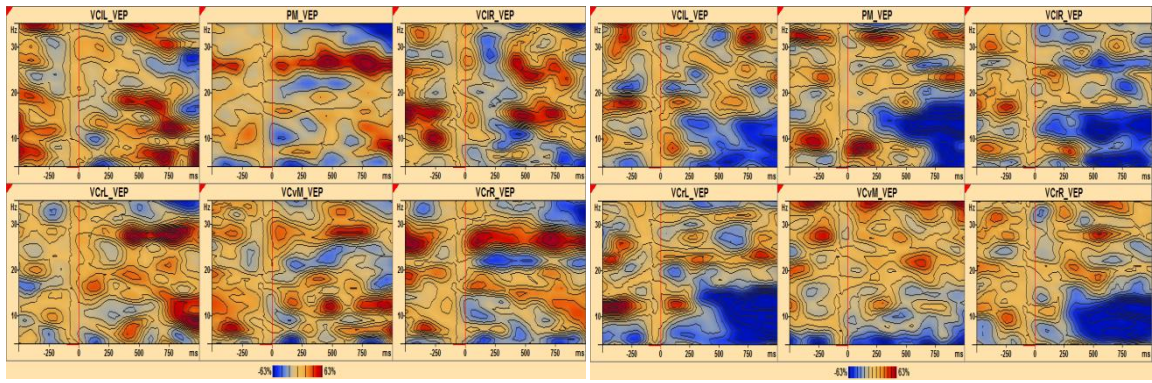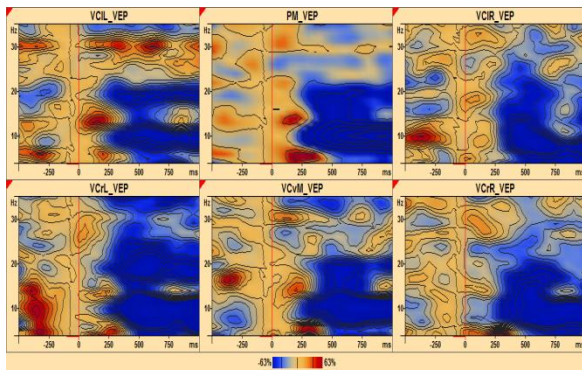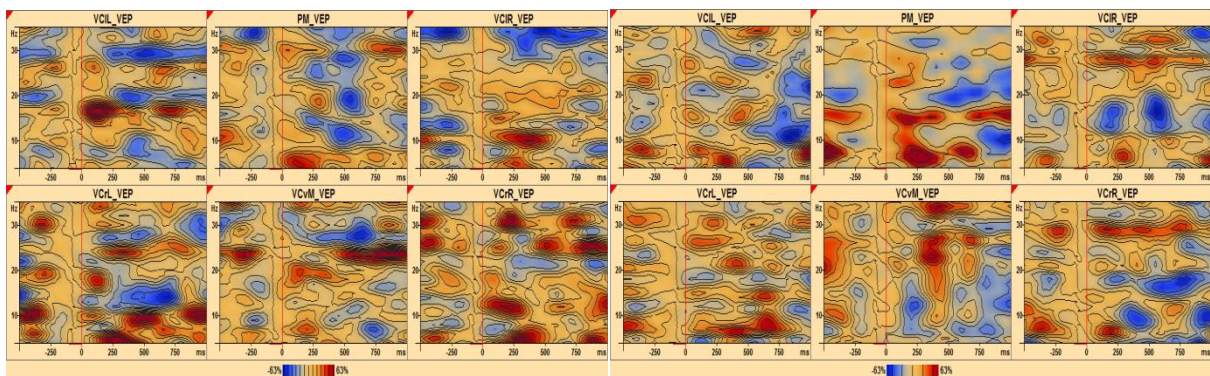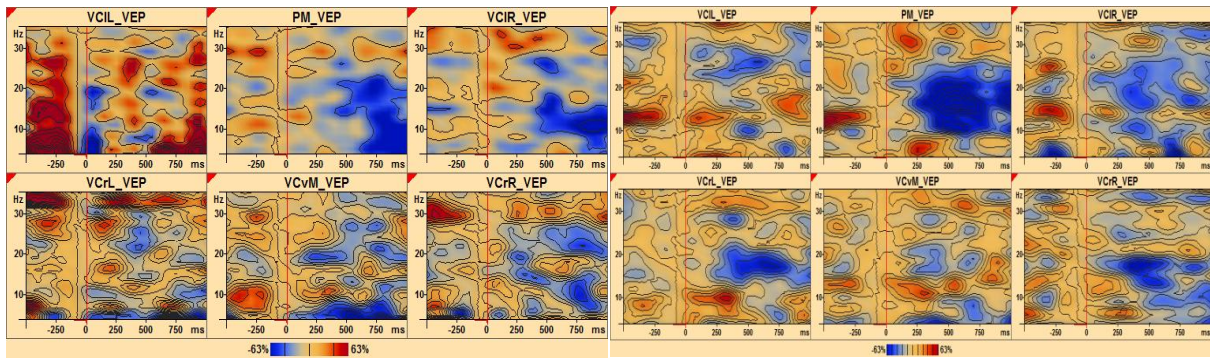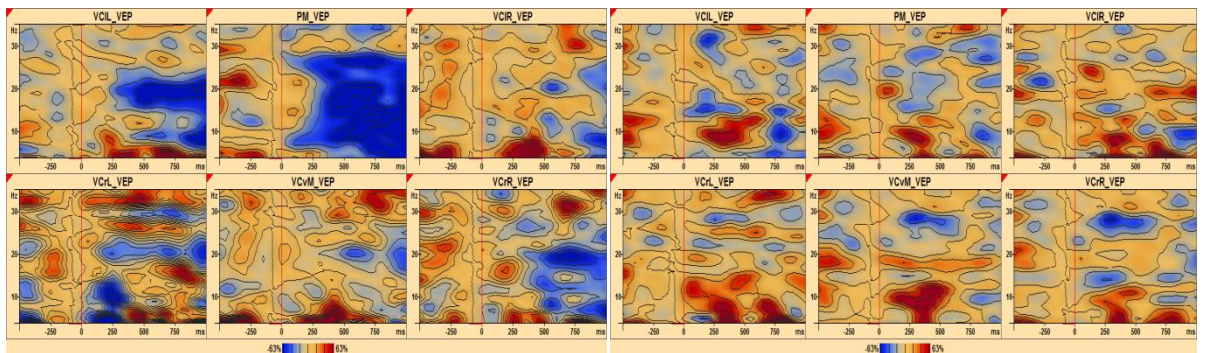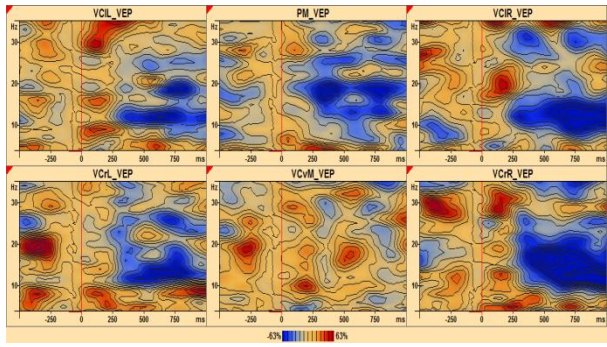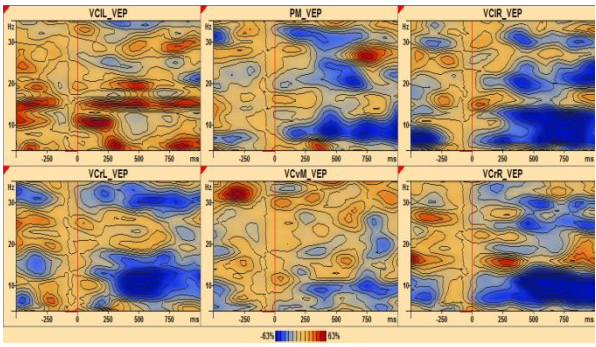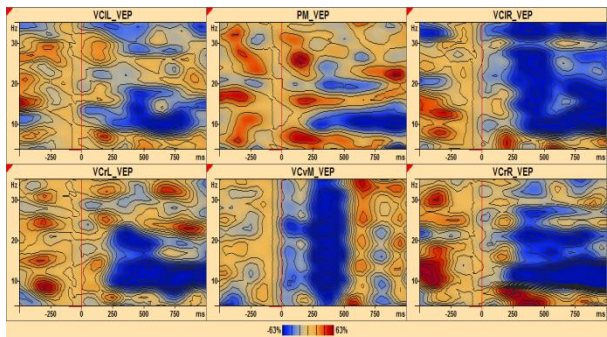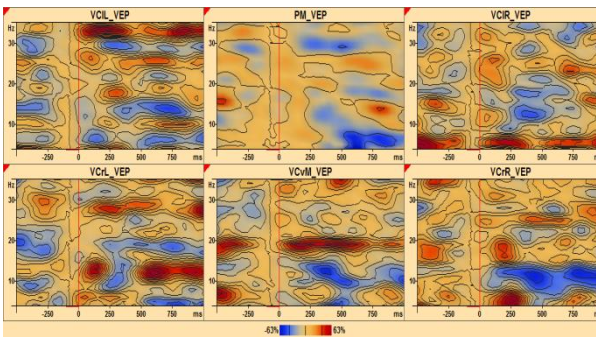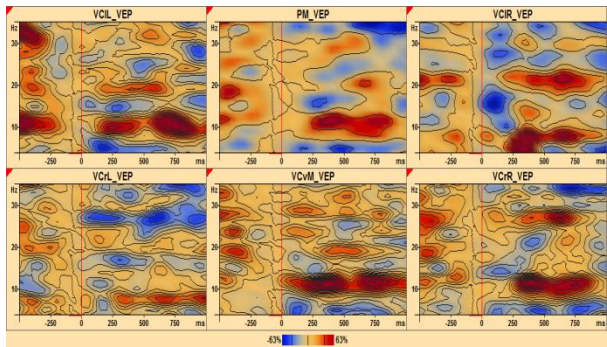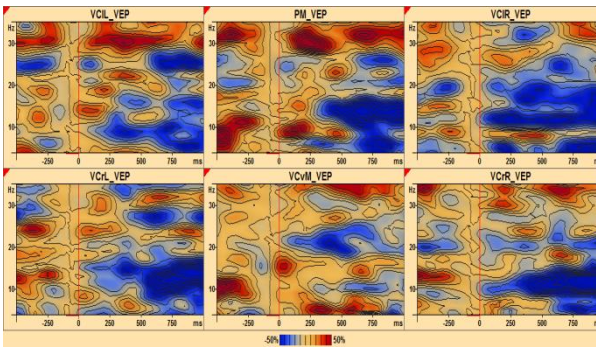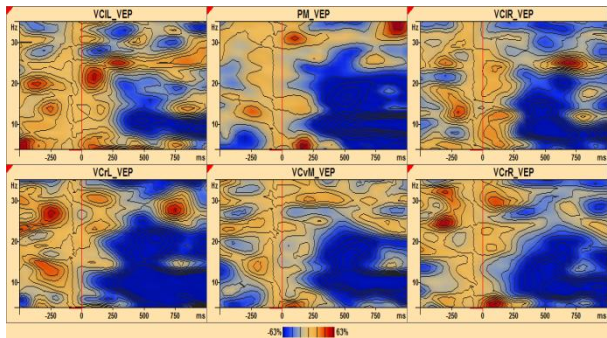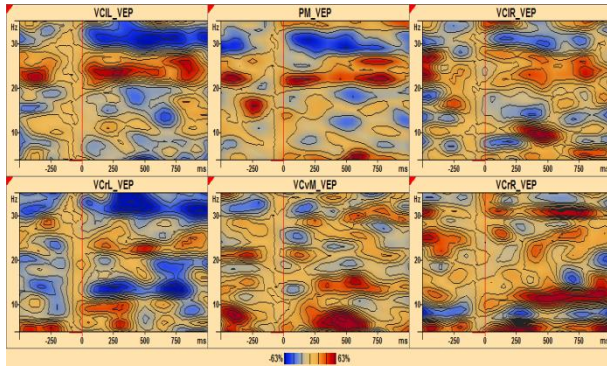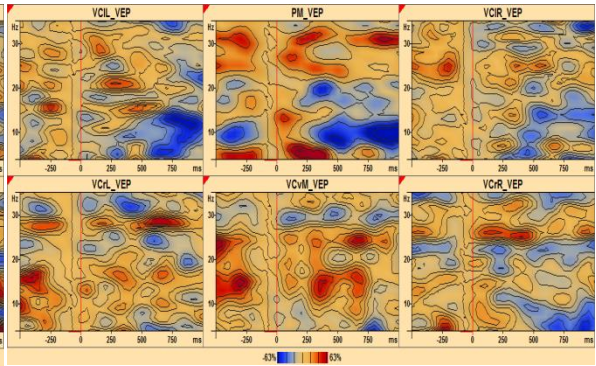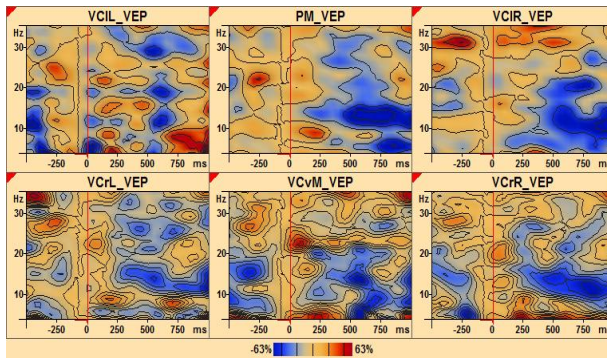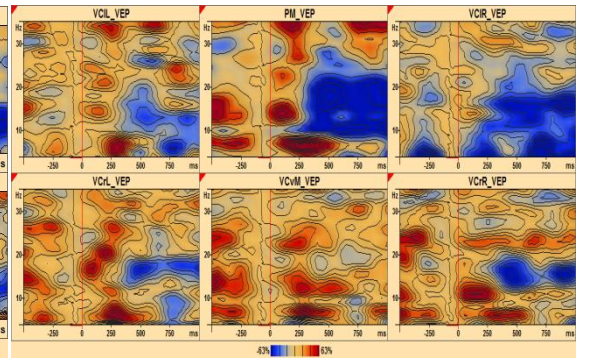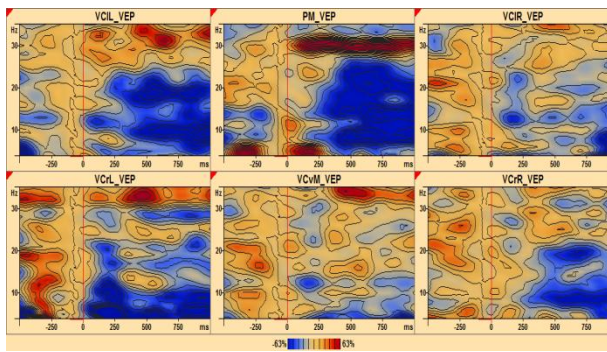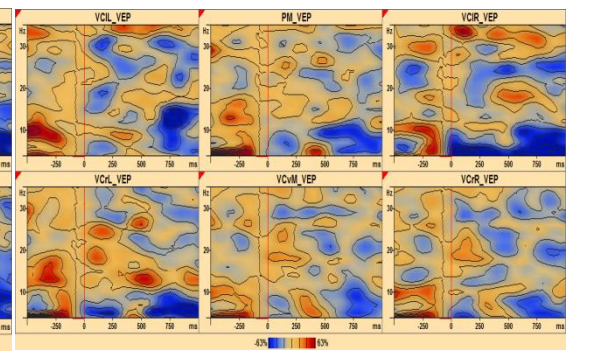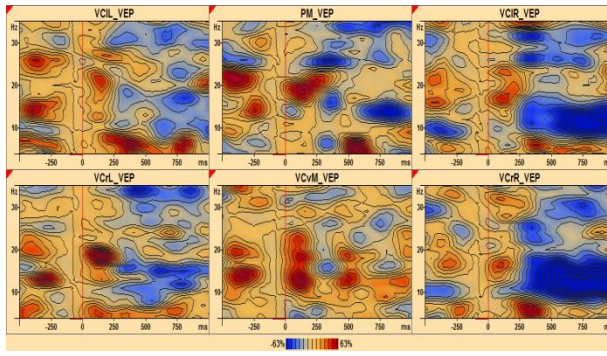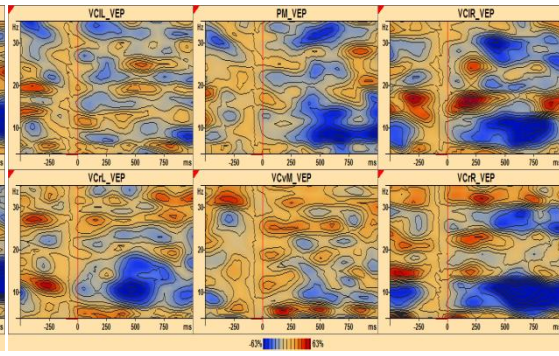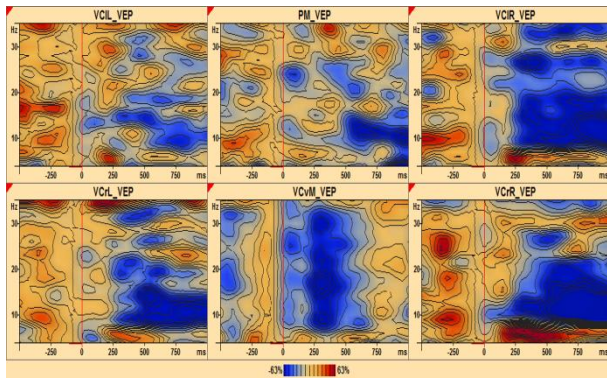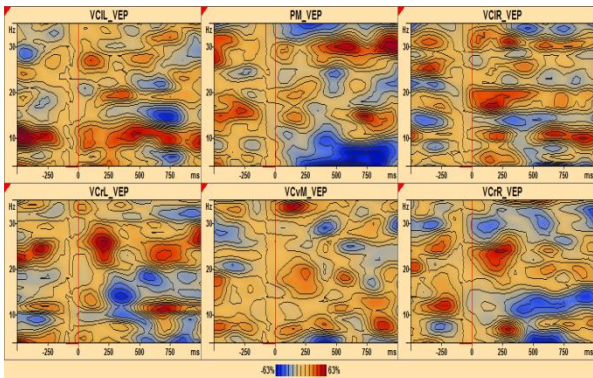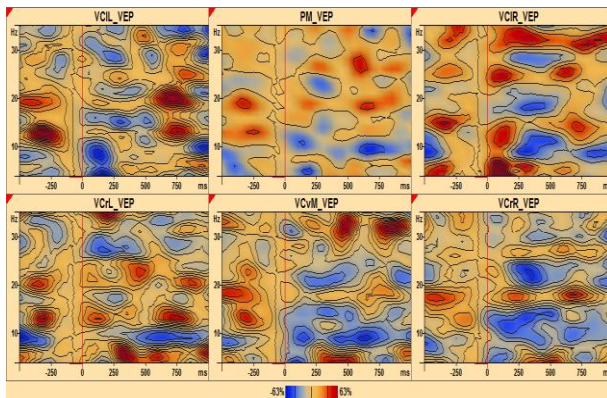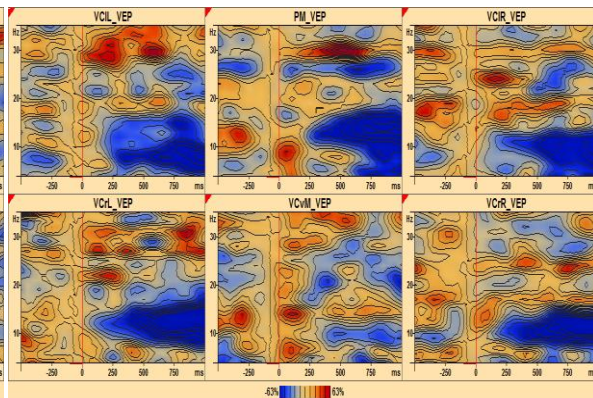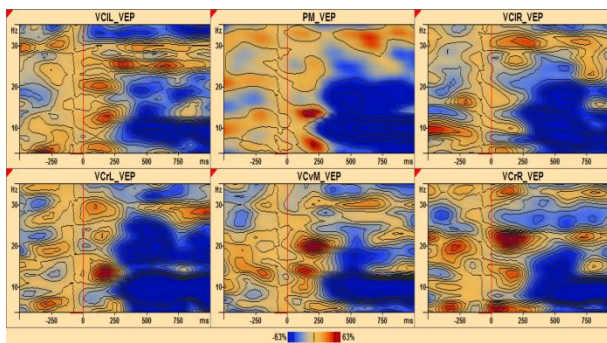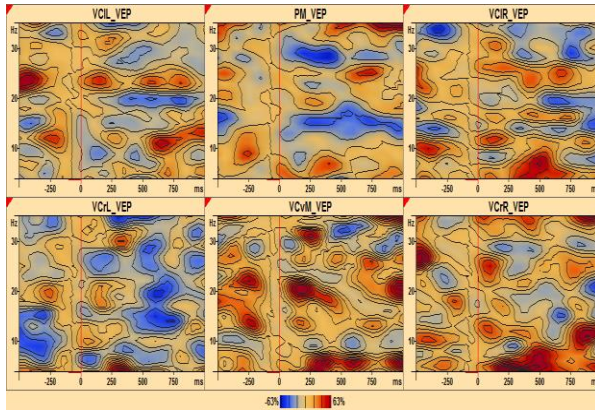
High Backward

A   B
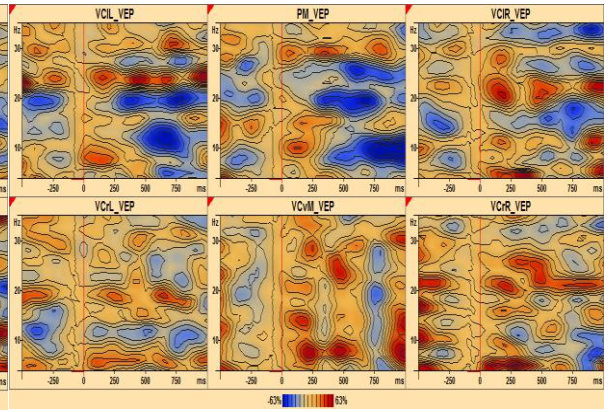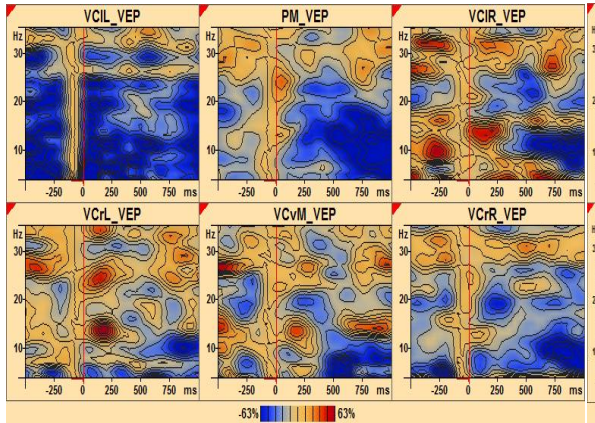
C   D
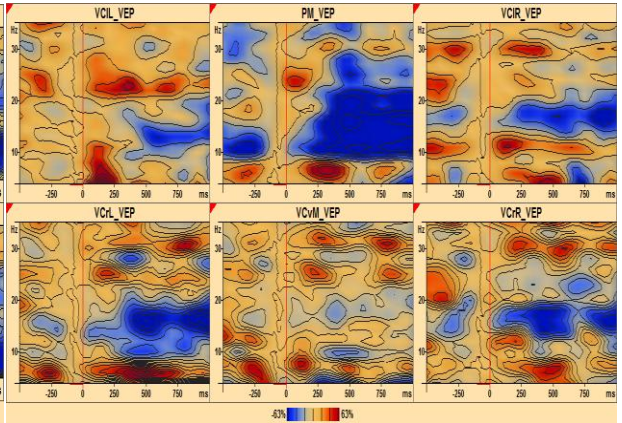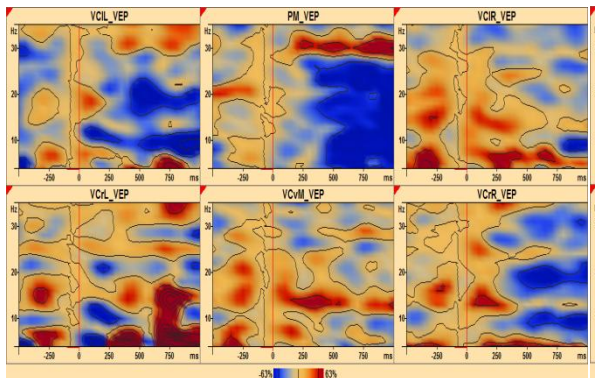
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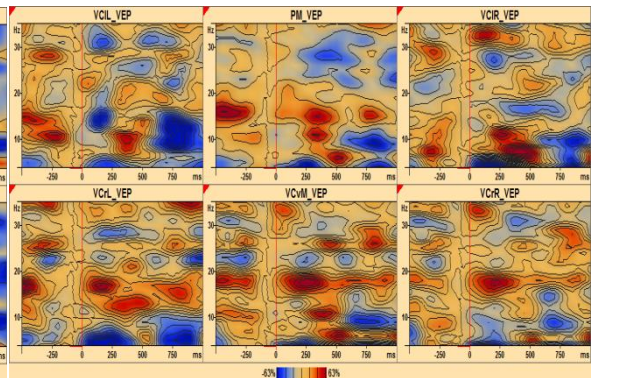
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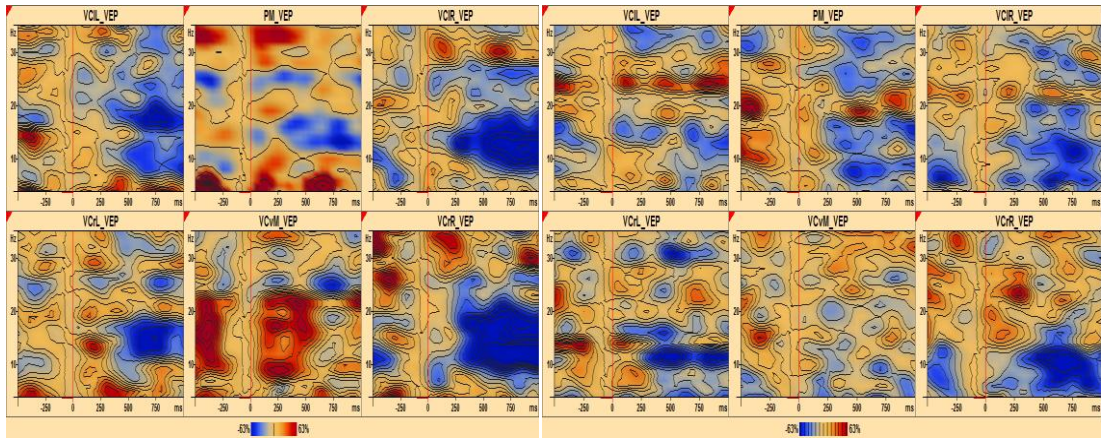
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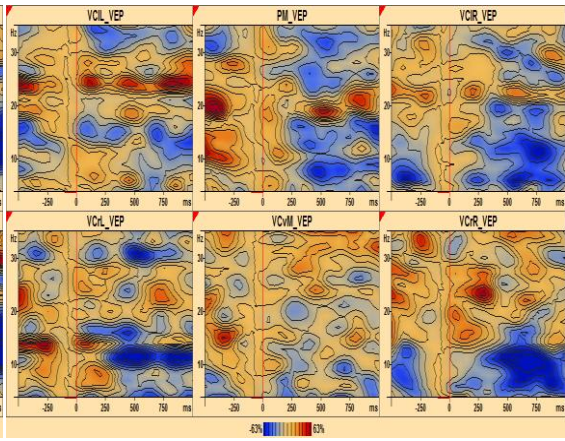
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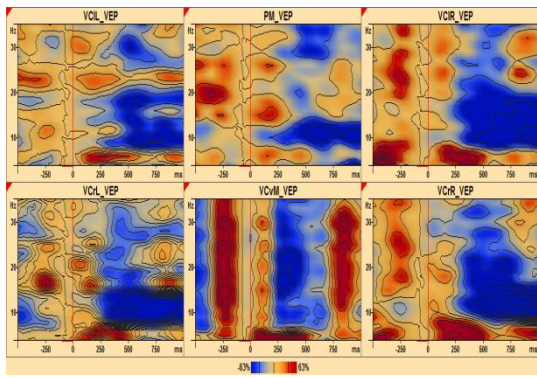
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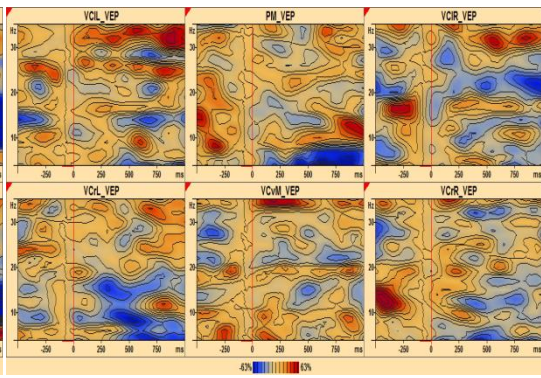
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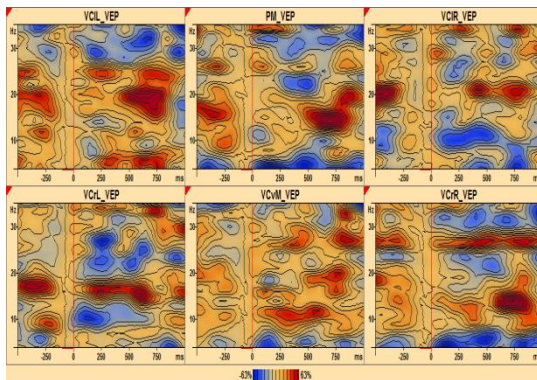
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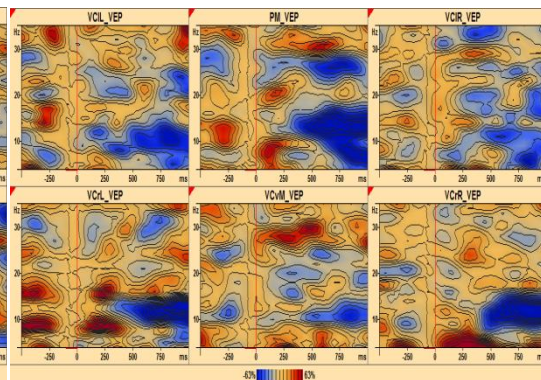
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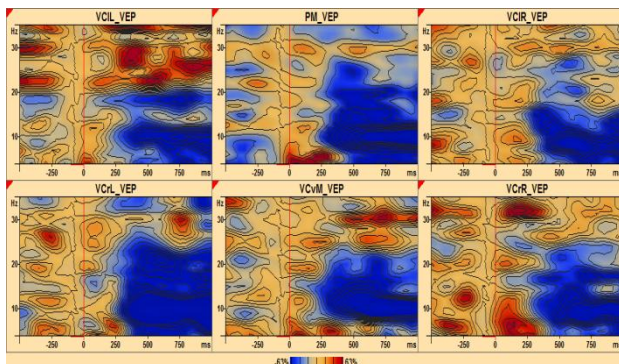
Static

A

B

C

D

E

F
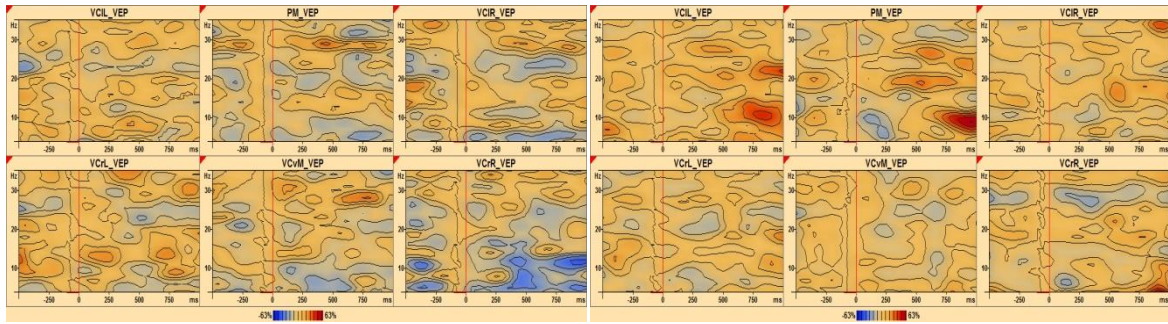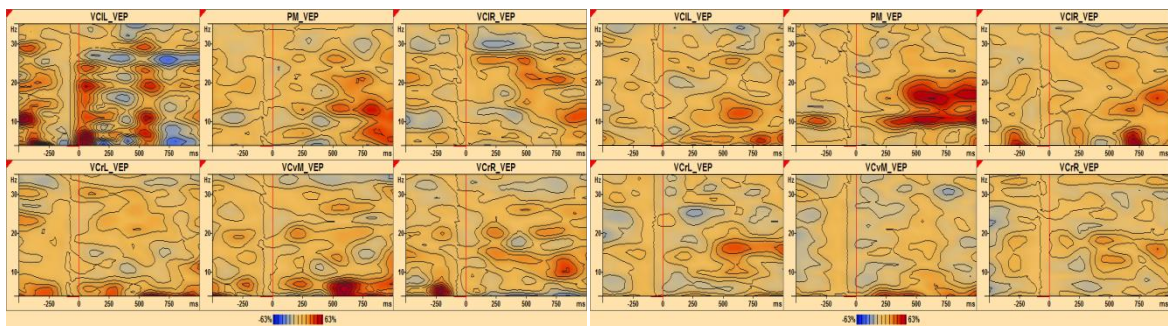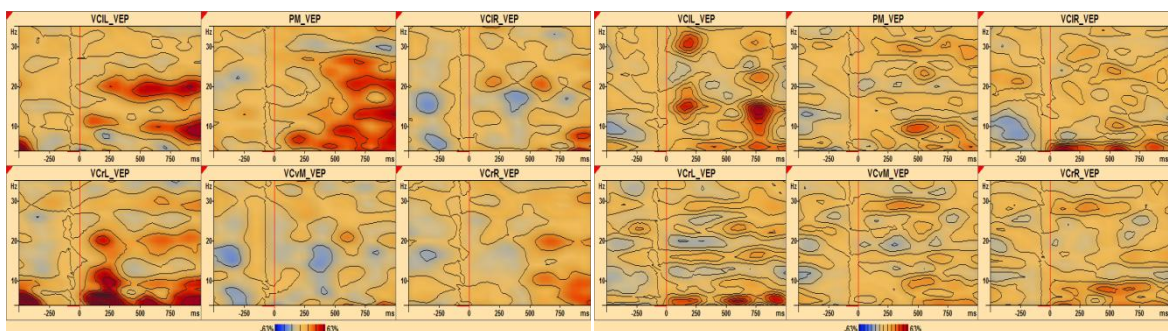
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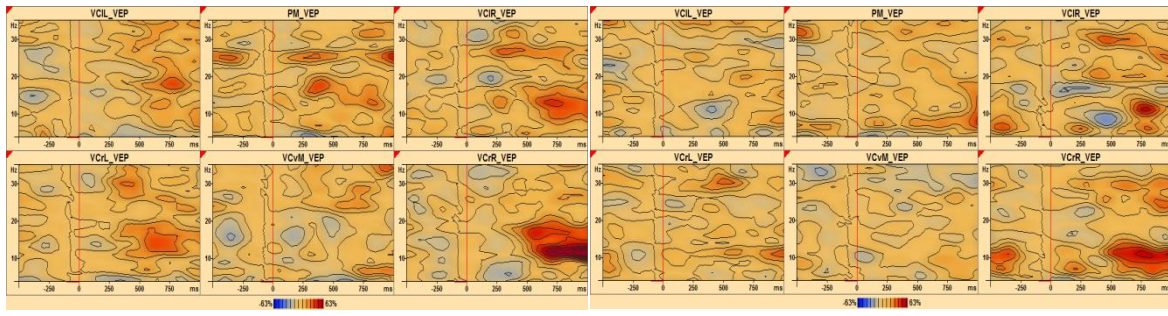
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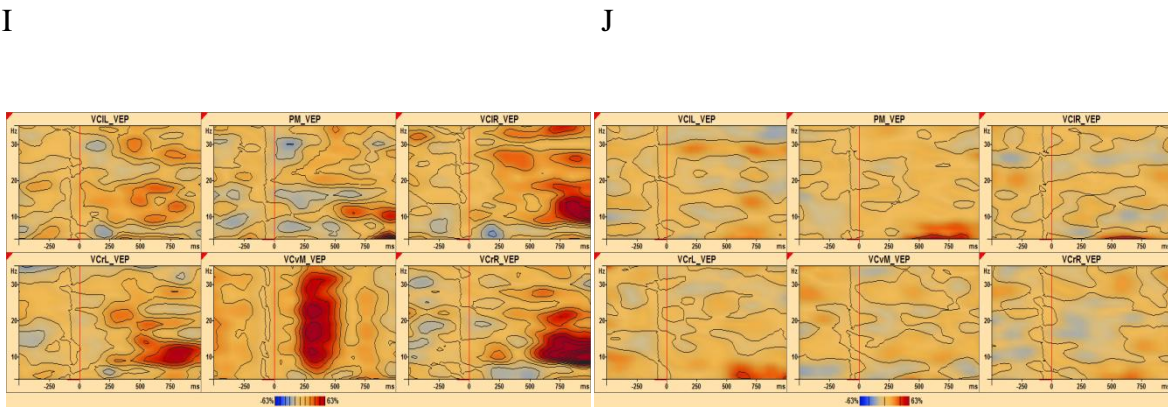
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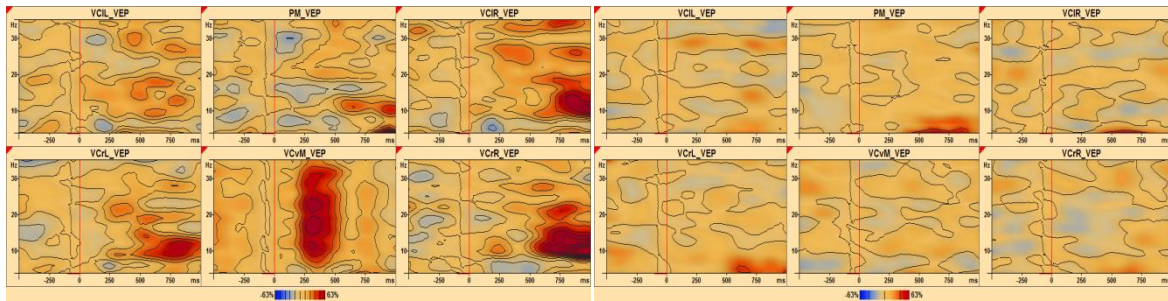
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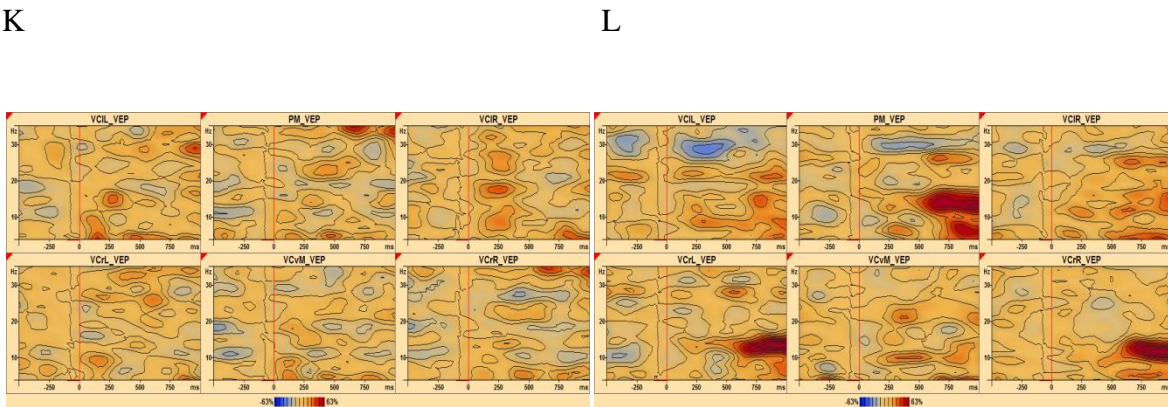
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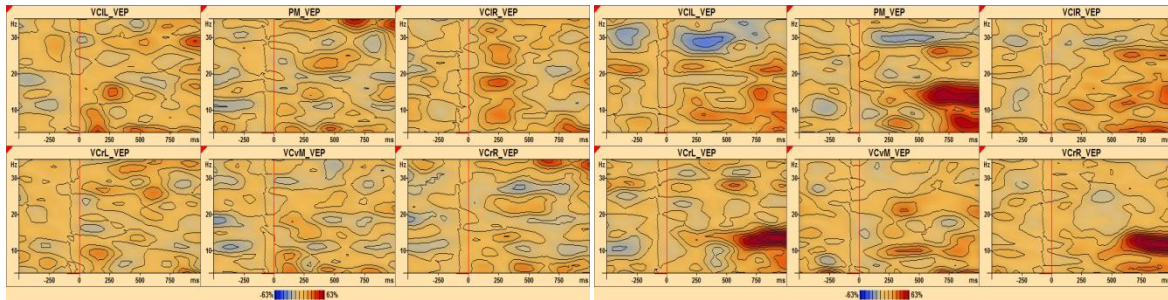
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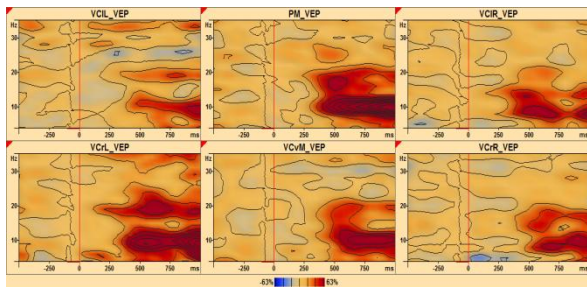
Appendix B

TSE probability maps (p<0.05) from all participants A-M in the low forward, low backward, high forward and high backward condition. Blue areas indicate a significant decrease in induced oscillatory activity (de-synchronizations) while the red areas indicate a significant increase in induced oscillatory activity (synchronizations). Epochs are set from -500 to 1000 ms, range 2 – 30 Hz. The motion conditions (low forward, low backward, high forward and high backward) were all compared to the static condition. Alpha de-synchronization can be seen in source PM, but also other sources. Sources used are: from top left to bottom right): VClL, PM, VClR, VCrL,VCvM, and VCrR. Red line indicates stimulus onset.

TSE Statistics

Low Forward

A   B
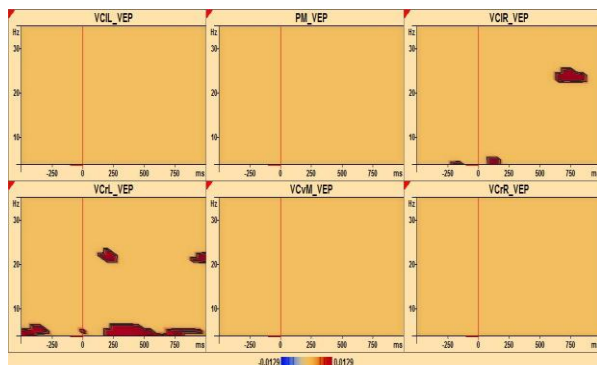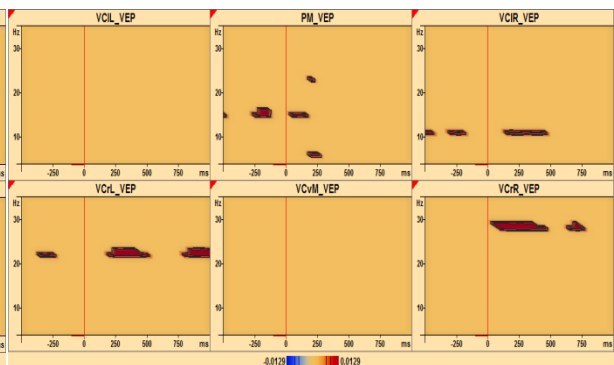
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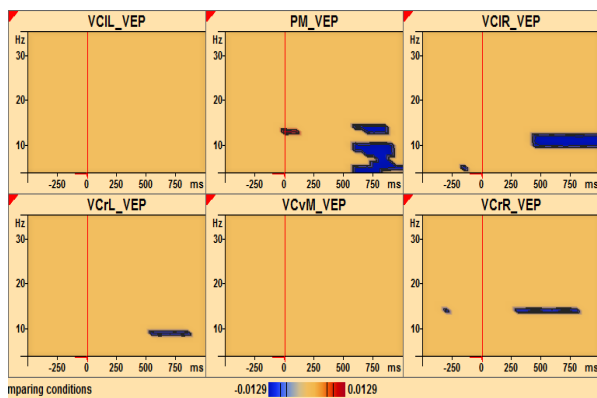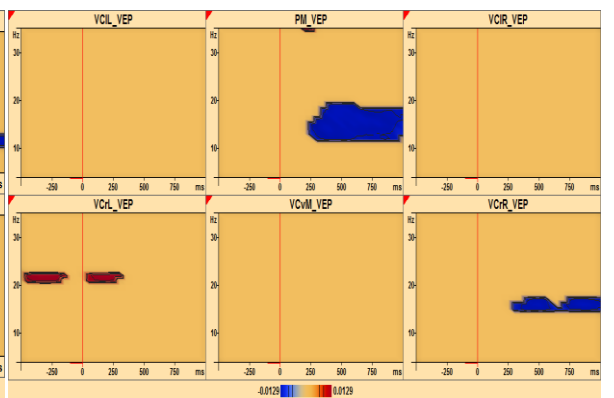
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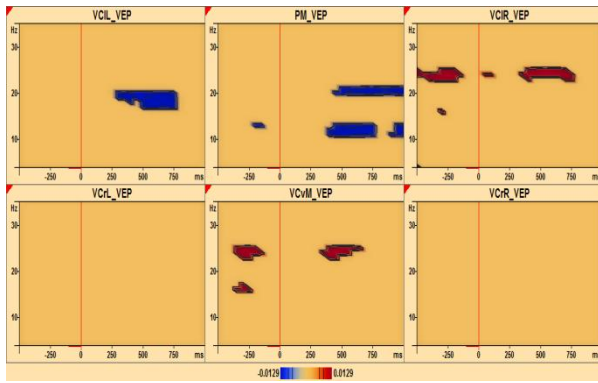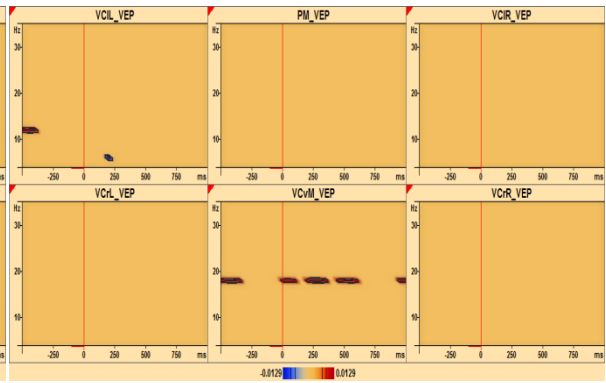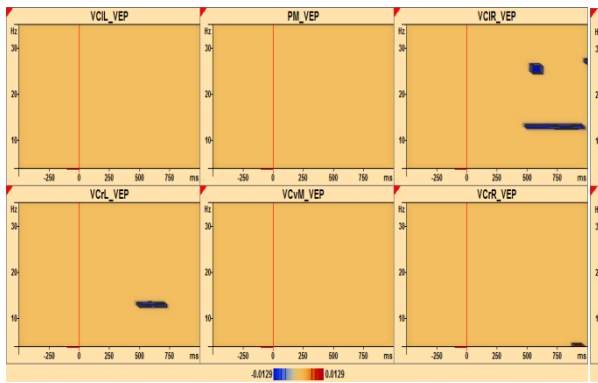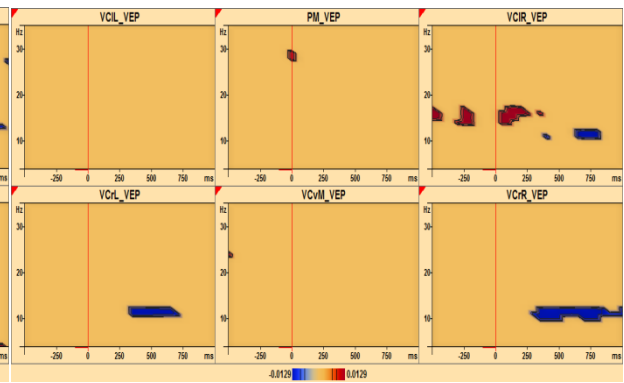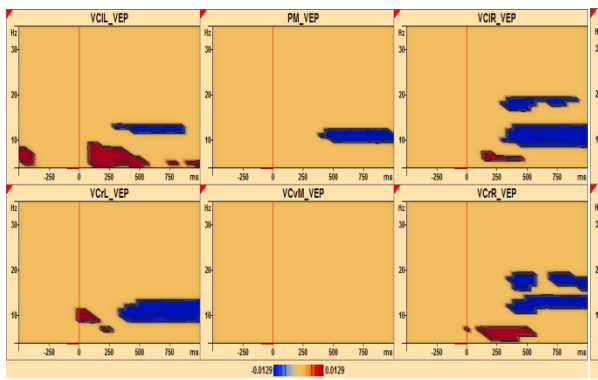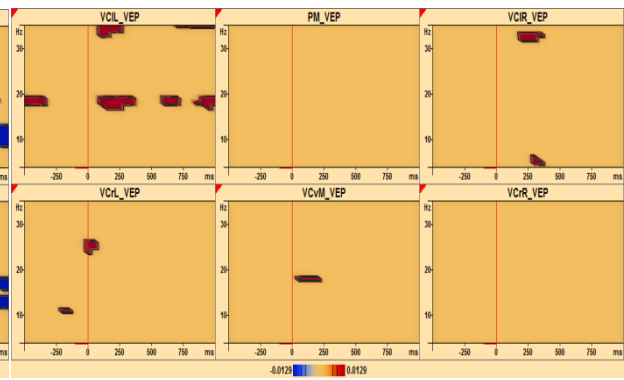
F

G

H

I

J

K

L

M

Low Backward

A

B

C

D

E

F

G

H

I

J

K

L

M

High Forward

A

B

C

D

E

F

G

H

I
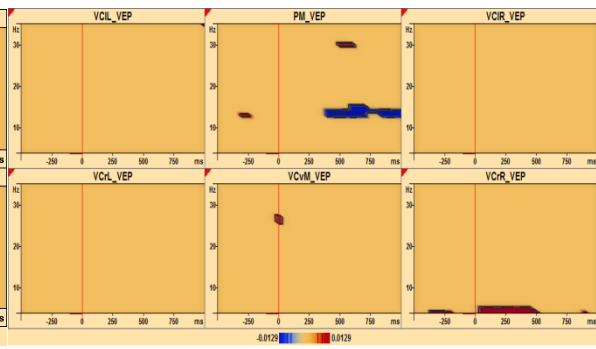

J

K

L

M
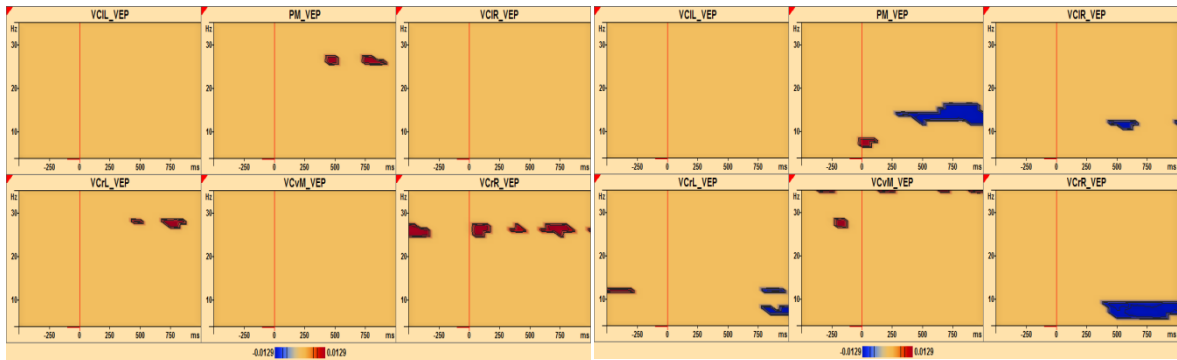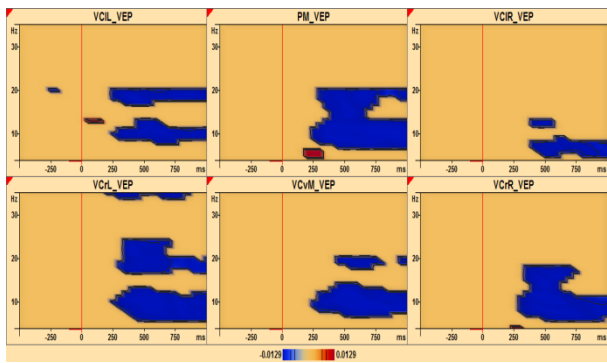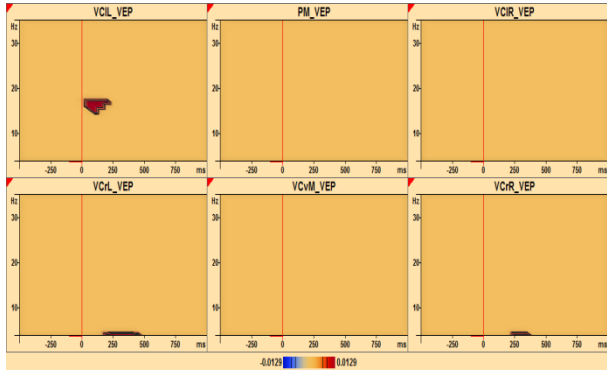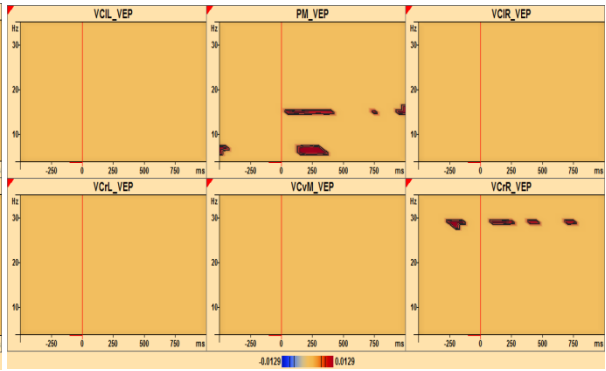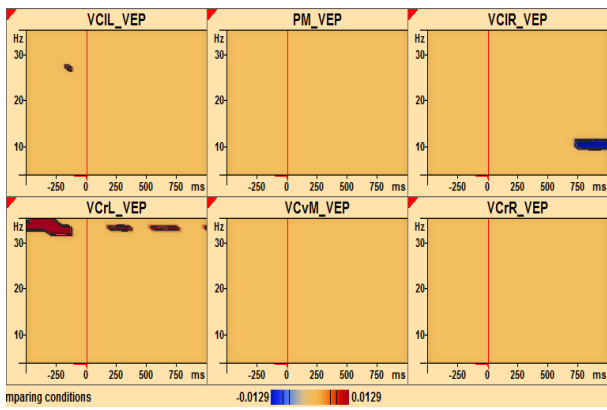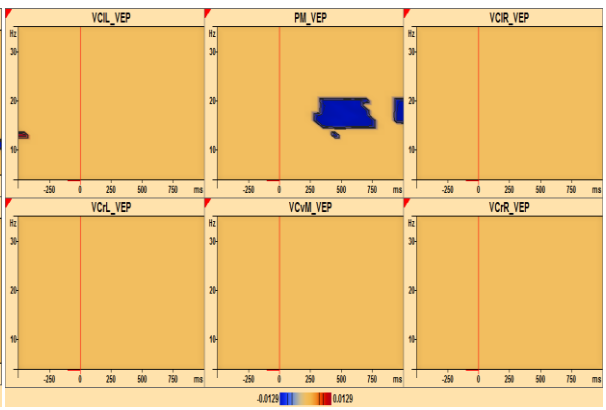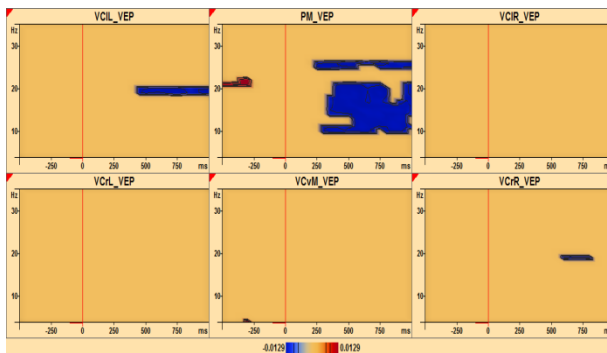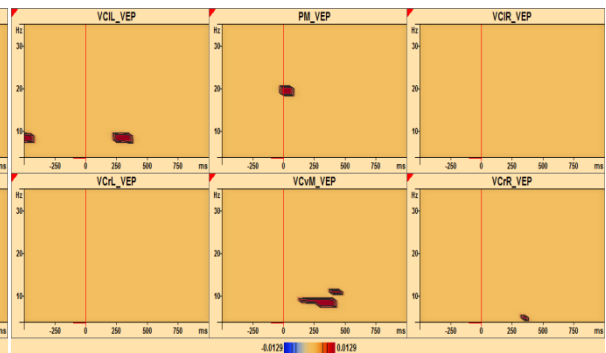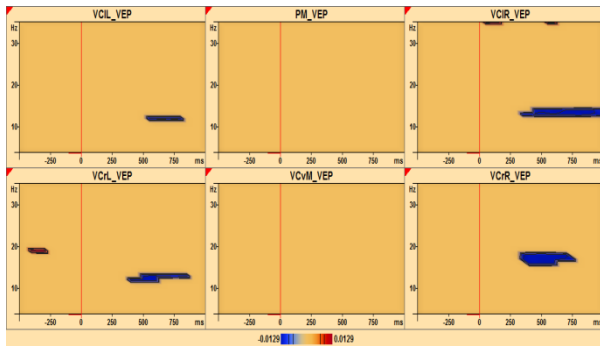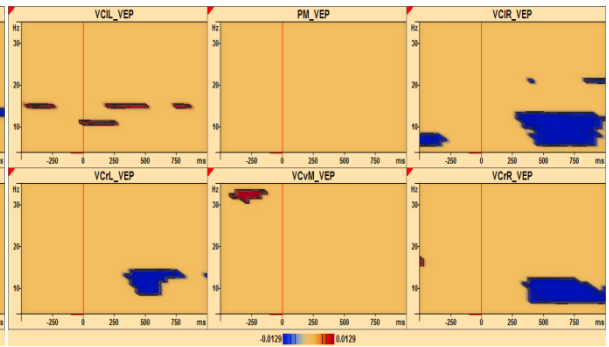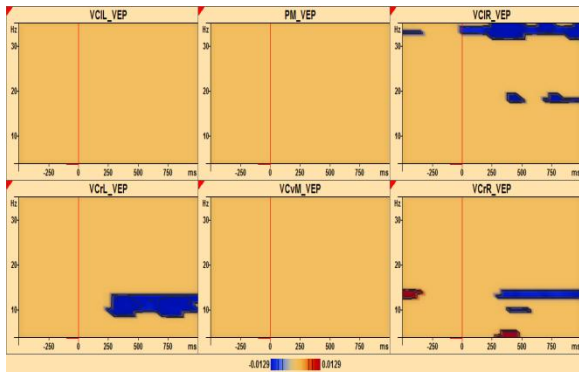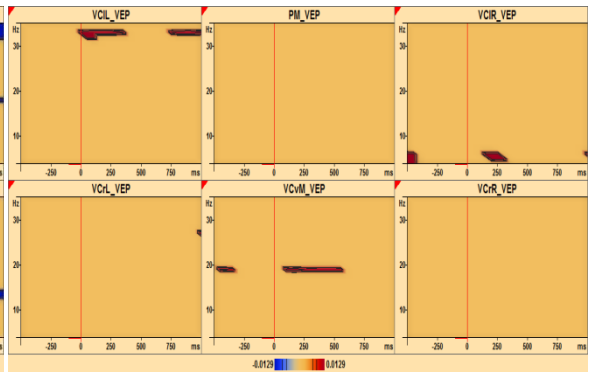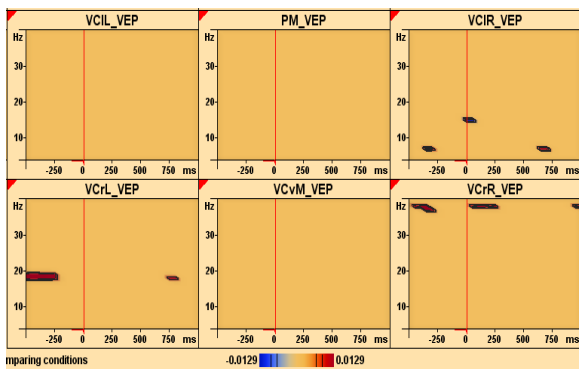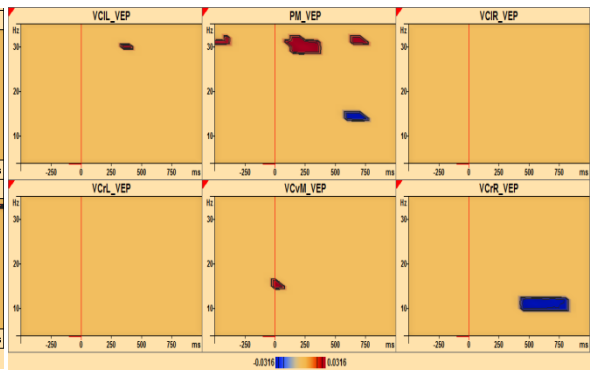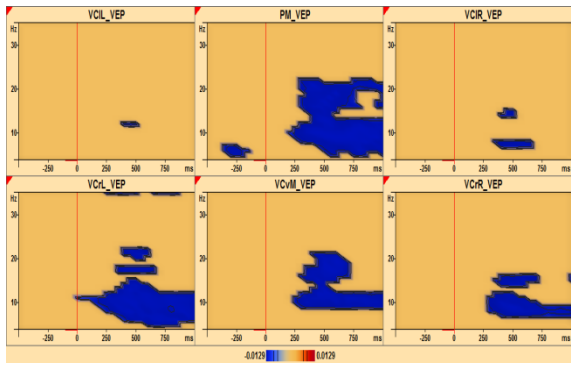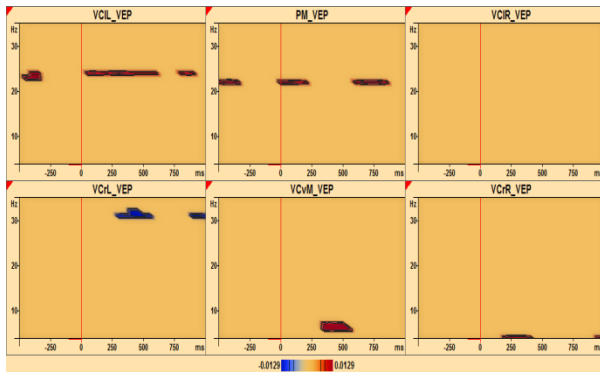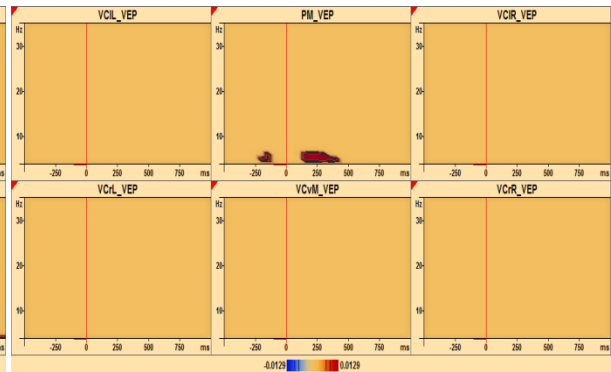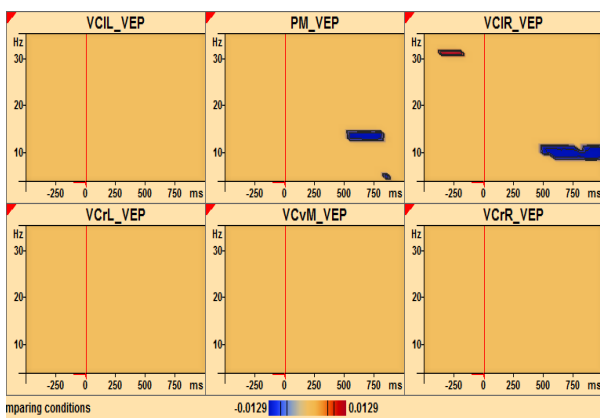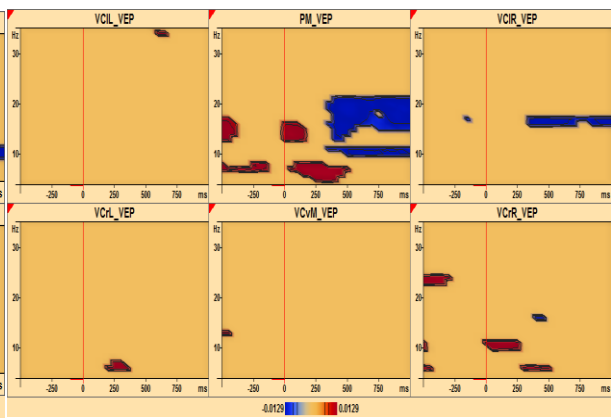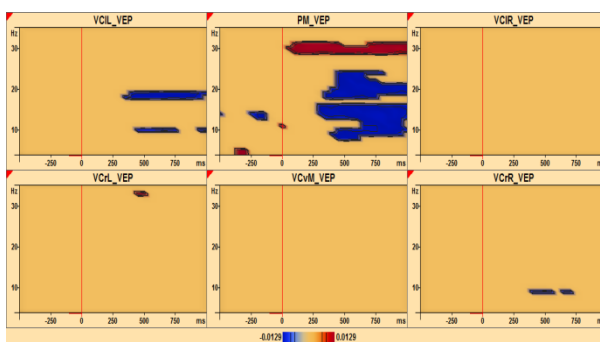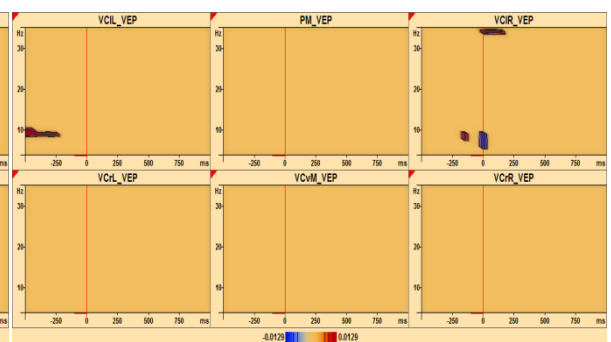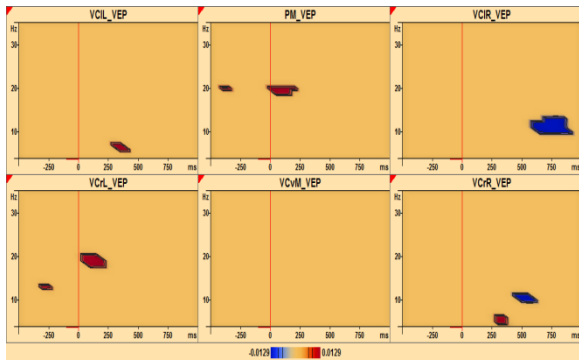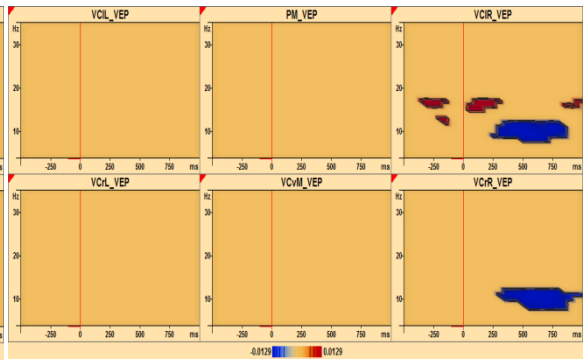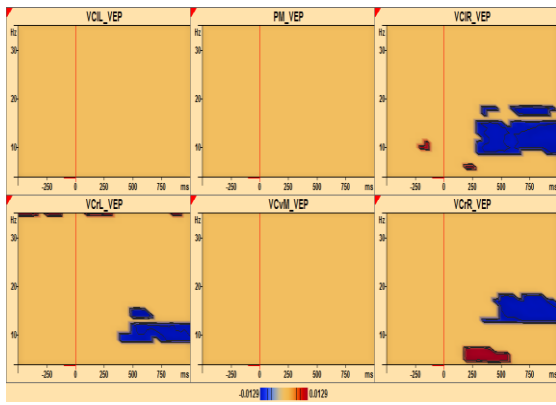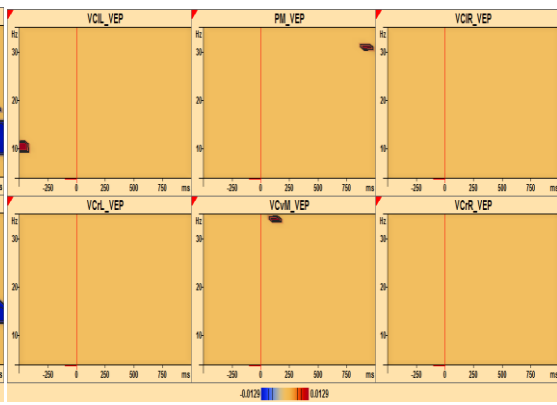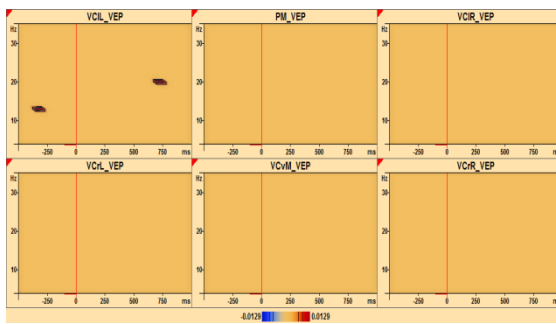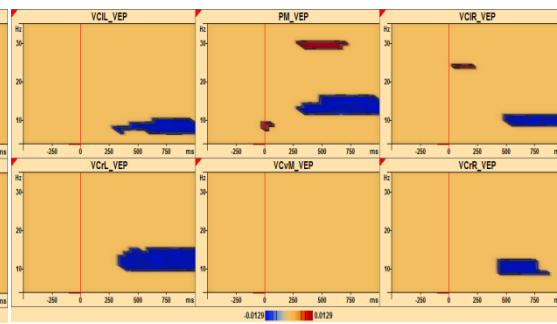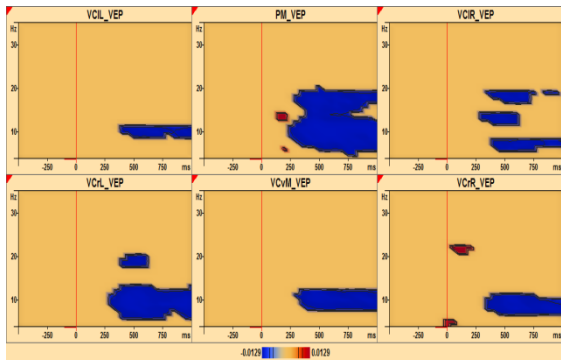
High Backward

A

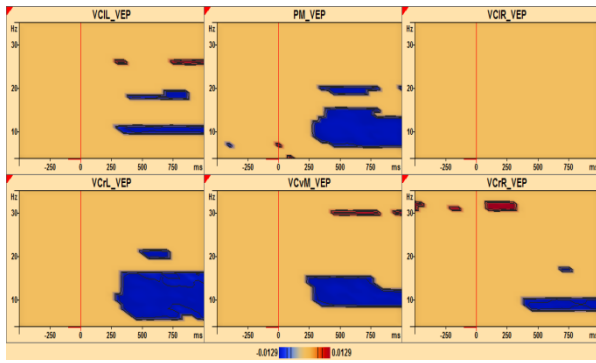B

C

D

E

F
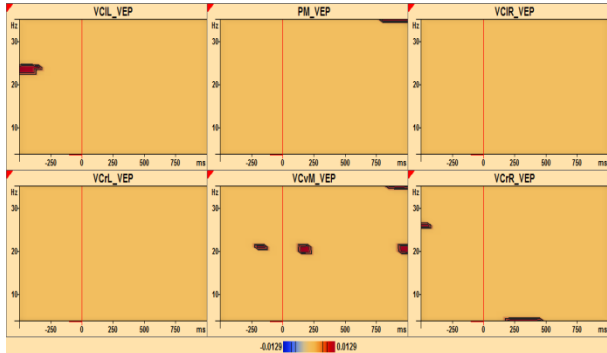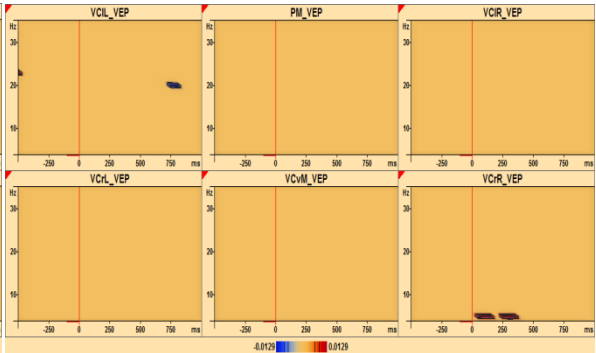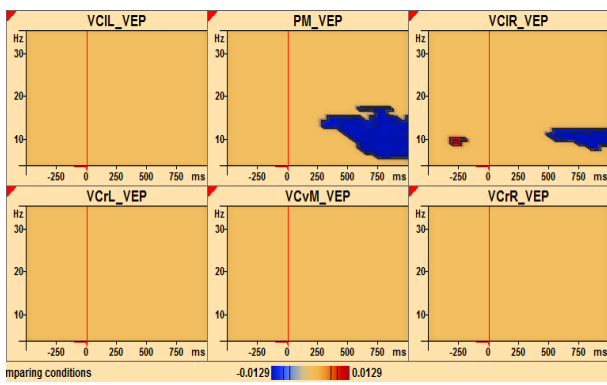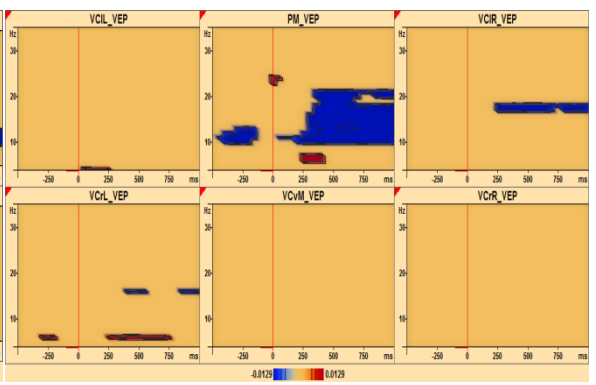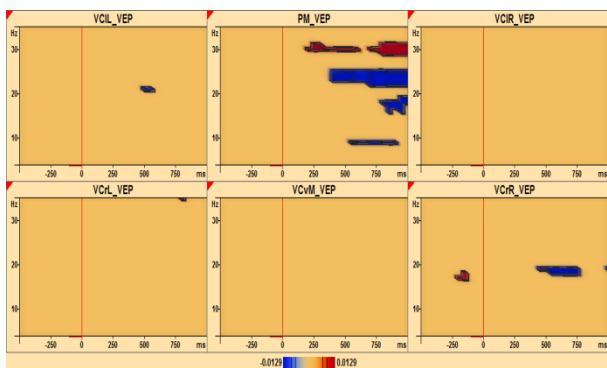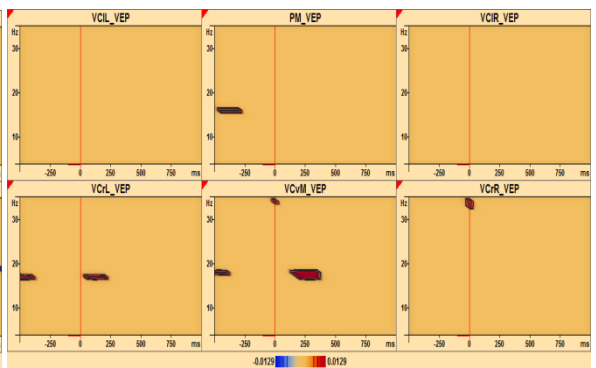
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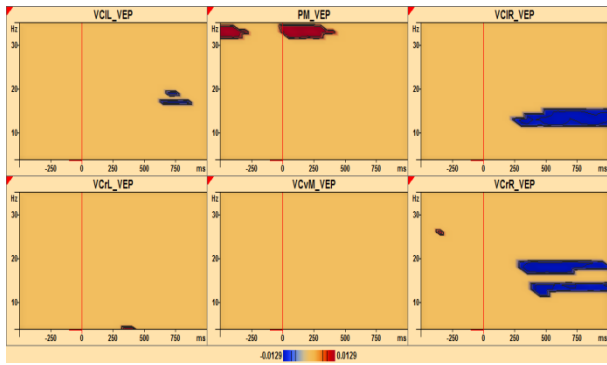
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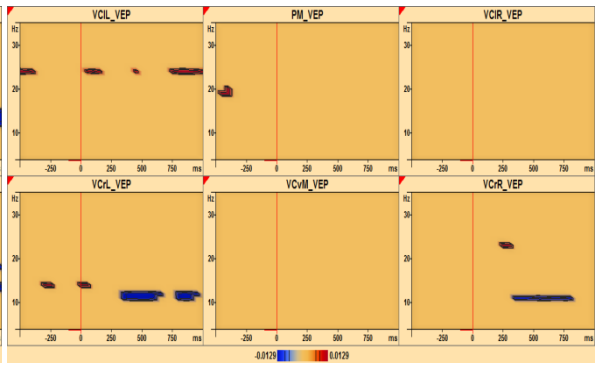
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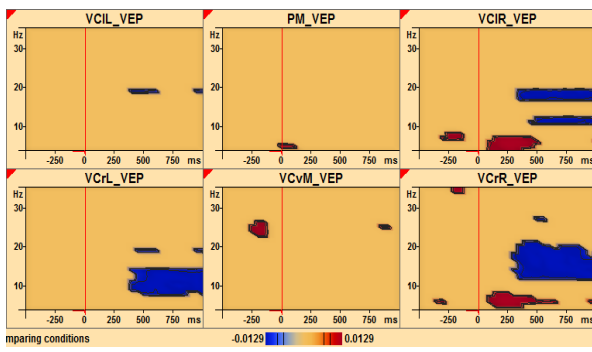
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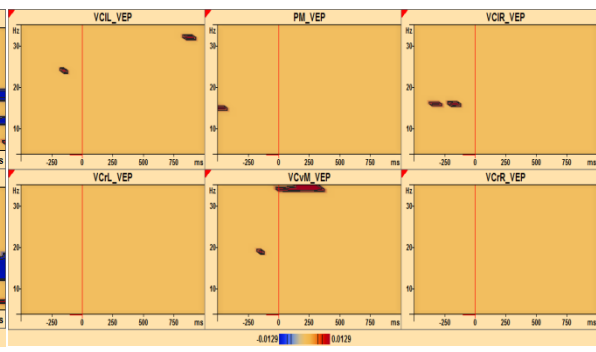
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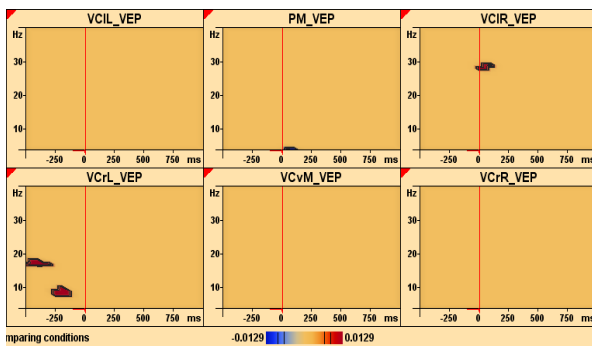
L

M

Appendix C

Averaged TSE plots of the low forward, low backward, high forward, high backward and static condition, and area of significant difference, p<0.05 in the low forward, low backward, high forward and high backward conditions, p<0.005 in sources VCIR, VClL, PM and VCrR. In the Low forward, high forward and high backward conditions alpha de-synchronizations can be seen from about 300 ms after stimulus onset and to the end of the epoch, while the static conditions show alpha synchronizations from about 500 ms after stimulus onset and to the end of epoch. The difference shows the area of significant difference between motion and static conditions from approximately 300 ms after stimulus onset, to, and beyond the end of the epoch. Epochs are set from -500 to 1000 ms, range 2 – 30 Hz, and measure unit was power (μV2).
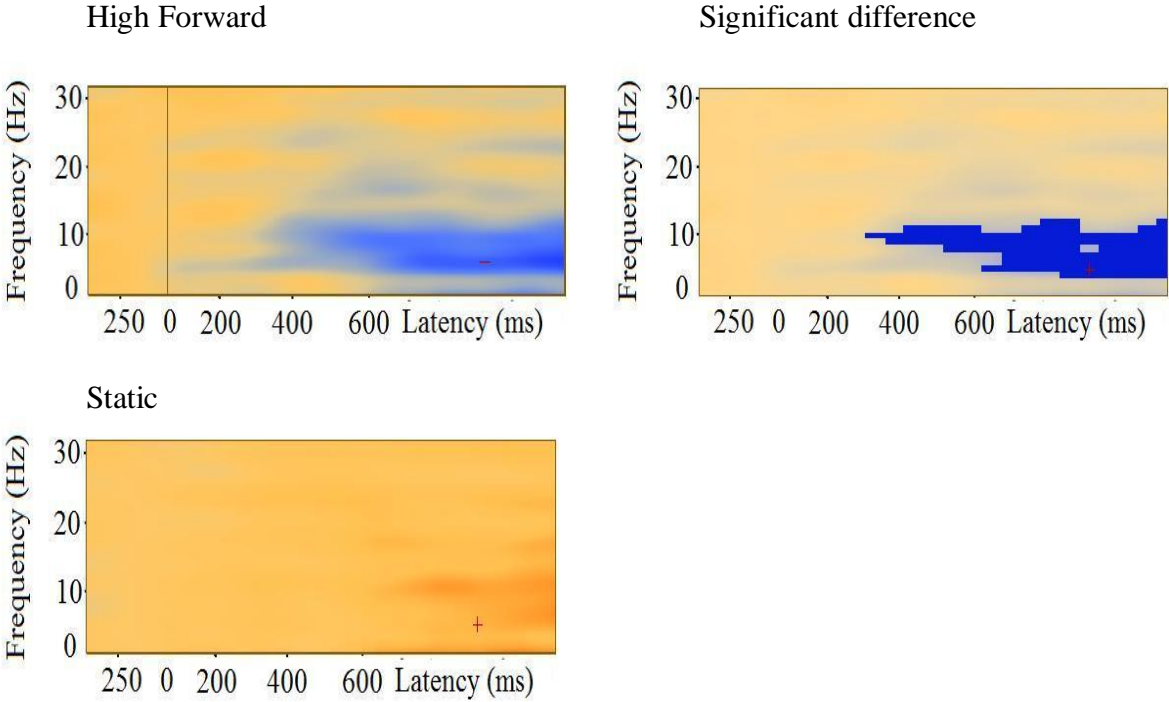
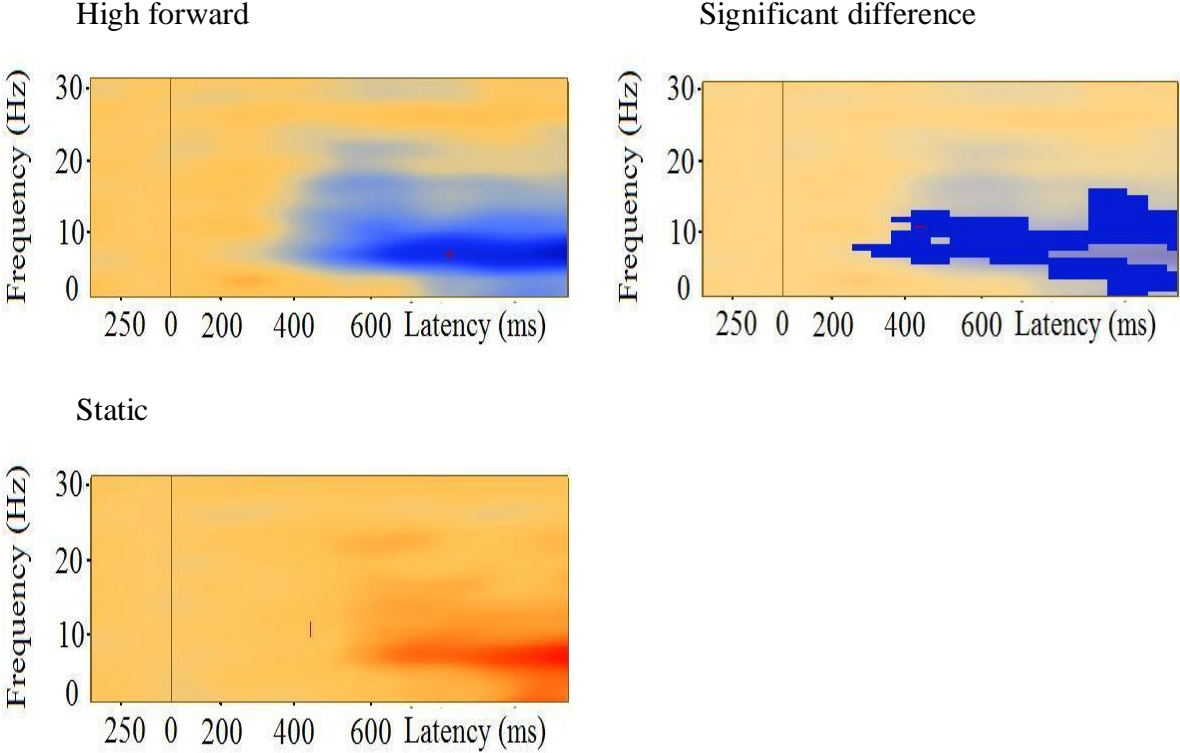Low speed forward, static and area of significant difference in source VCrR

Low Forward

Significant difference
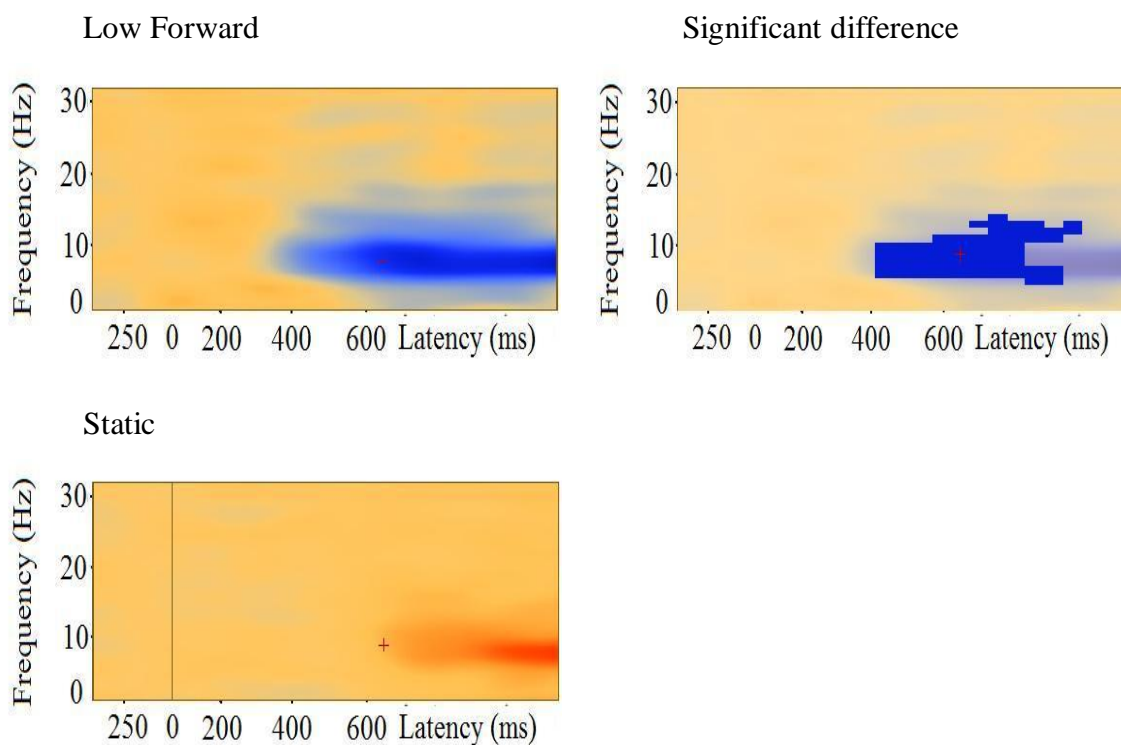
Static

Low speed backward, static and area of significant difference in source PM

Low speed

Signficant difference
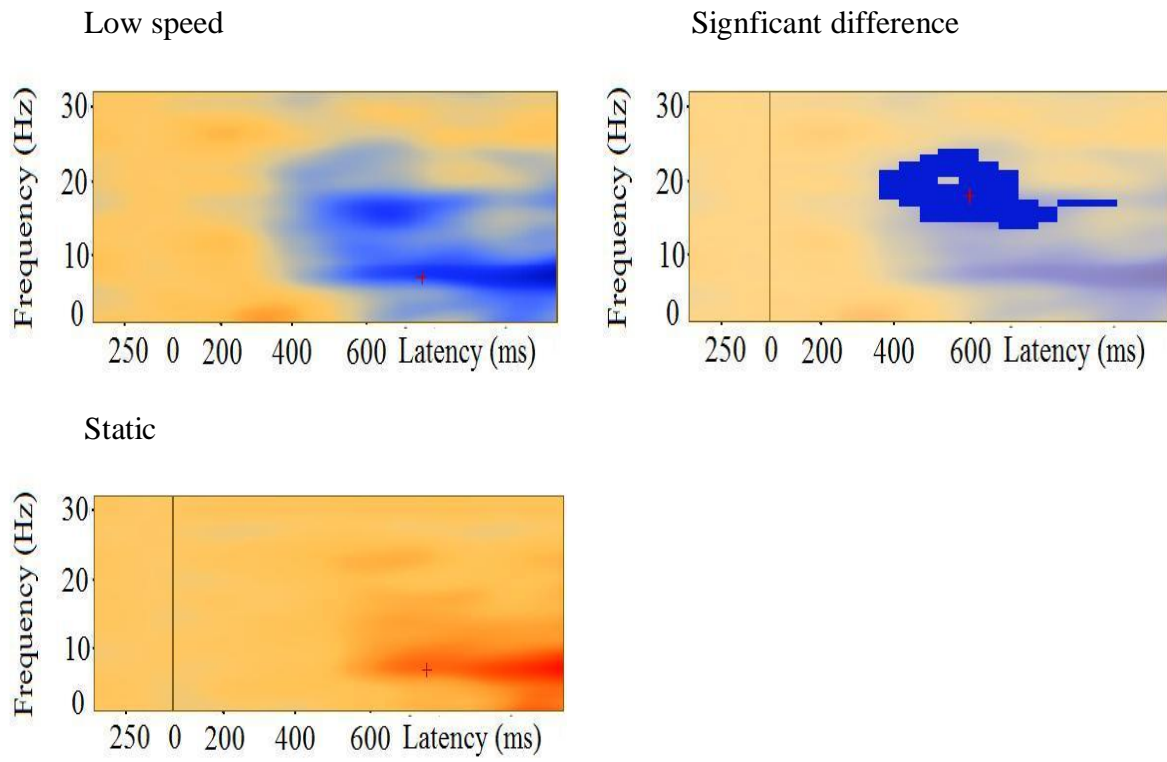
Static

High speed forward, static and area of significant difference in source VCIR

High Forward

Significant difference

Static

High speed forward, static and area of significant difference in source PM

High forward

Significant difference

Static

High speed backwards, static and area of significant difference in source VClL

High backward

Significant difference

Static