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Evidence that smooth pursuit velocity, not eye position, modulates alpha and beta oscillations in human middle temporal cortex

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Abstract

Suppression of 5-25 Hz oscillations have been observed in MT+ during pursuit eye movements, suggesting oscillations that play a role in oculomotor control and/or the integration of extraretinal signals during pursuit. The amplitude of these rhythms appears to covary with head-centred eye position, but an alternative is that they depend on a velocity signal that lags the movement of the eyes. To investigate, we explored how alpha and beta amplitude changes related to ongoing eye movement depended on pursuit at different eccentricities. The results revealed largely identical patterns of modulation in the alpha and beta amplitude, irrespective of the eccentricity at which the pursuit eye movement was performed. The signals we measured therefore do not depend on head-centred position. A second experiment was designed to investigate whether the alpha and beta oscillations depended on the direction of pursuit, as opposed to just speed. We found no evidence that alpha or beta oscillations depended on direction, but there was a significant effect of eye speed on the magnitude of the beta suppression. This suggests distinct functional roles for alpha and beta suppression in pursuit behaviour.

Keywords

Smooth pursuit, magnetoencephalography, extra-retinal signals, MT+/MST, neuronal oscillations

Abbreviations

BOLD   Blood oxygen level dependent

EEG   Electroencephalography

EOG   Electrooculography

MEG   Magnetoencephalography

MRI   Magnetic resonance imaging

MT/MT+   Middle temporal cortex

MST   Medial superior temporal cortex

ROI   Region-of-interest

SAM   Synthetic aperture magnetometry

SPM   Statistical parametric map

Introduction

Cortical oscillations are a pervasive phenomenon in neuroscience and are thought to subserve a number of cognitive, sensory and motor processes. Oscillatory changes in human MT+ have been shown to accompany smooth eye pursuit, but their functional role is still not completely understood. In MST, a majority of neurons that display a pursuit-related response (i.e. those that do not show a response to retinal motion) have been shown to code for eye velocity, whilst only a small minority display have any sensitivity to head-centred eye position (Ilg & Thier, 2003). We previously reported (Dunkley, Freeman, Muthukumaraswamy, & Singh, 2011) that suppression of the 5-25 Hz response in MT+, a correlate of increased cortical activity, covaried with eye position, but other studies have shown that eye speed was the dominant signal in animal (Churchland & Lisberger, 2005) and human studies (Nagel, Sprenger, Hohagen, Binkofski, & Lencer, 2008; Nagel et al., 2006). However, given the paradigm we used, it was not possible to explain this discrepancy because eye position and speed covaried.

The first experiment presented here was therefore designed to tease these two stimulus parameters apart by presenting pursuit targets with identical velocity profiles at different mean eccentricities (centre, left or right). If oscillatory activity coded primarily for eye position during ongoing pursuit, we might expect to see distinct amplitude envelope profiles for alpha and beta activity dependent on the eccentricity of the pursuit cycle. For example, when engaging in a pursuit cycle in the contralateral hemifield with respect to the recording site, relatively *greater* suppression (decrease in amplitude) of the activity in MT+ might be expected; and equally, *less* suppression might be expected when pursuing a target in the ipsilateral visual hemifield. Conversely, if the changes in the amplitude envelopes do not depend on eye position, then these macroscopic signals might reflect some other aspect of the pursuit movement, such as speed, that is common to all eccentricities tested.

To our knowledge, there have been only a handful of neuroimaging papers on how pursuit velocity modulates activity in MT+. For example, Nagel et al. (2008) reported an increasing cortical activation (measured via the blood oxygen level-dependent, effect; BOLD) observed for increasing stimulus velocity (Nagel, et al., 2008; Nagel, et al., 2006). However, they in fact demonstrated *speed*-related activity because BOLD signals were collapsed across the direction of pursuit.

Extraretinal signals in MST characterised by activity in neurons with a preference for the ipsilateral pursuit are thought to make up the majority of neurons in MST (Ilg & Thier, 2003;

Ono & Mustari, 2006). We therefore performed a second experiment to test whether oscillatory changes in human MT+ depend on relative direction or just speed, by examining potential biases in oscillatory amplitude for ipsi- or contra-versive pursuit. Furthermore, we examined whether there is any evidence of a directional bias in alpha and beta for different pursuit directions, which might reveal a specific mechanistic role for these rhythms.

Given the link between spike-rate, the BOLD effect and low-frequency suppression (Mukamel et al., 2005), and animal data that show the existence of pursuit-sensitive velocity-dependent neurons in MT+ (Ono & Mustari, 2006), we hypothesised that alpha and beta suppression in unilateral MT+ would increase with increasing ipsiversive pursuit velocity.

Methods

Experiment 1

Participants

Eighteen healthy participants (13 females, mean age = 23 years) completed Experiment 1. All had given prior informed consent, had normal or correct-to-normal visual acuity and no history of neurological disorders. All experimental procedures were approved by the Cardiff University School of Psychology Ethics Committee.

Design and procedure

Figure 1 here

Figure 1 shows the experimental protocol for Experiment 1, which consisted of 3 conditions. In the first condition, 'central pursuit', participants were required to make sinusoidal horizontal pursuit eye movements by tracking a faint dot in the central portion of the screen (0.5 Hz frequency, amplitude ±5º). In the second 'right pursuit' condition, participants made horizontal pursuit eye movements that took place completely in the right hemifield; that is, in a head-centred reference frame, starting at 7.5º eccentricity, with an amplitude of ±5º and a frequency of 0.5 Hz (otherwise identical to condition 1, 'central pursuit'). In the third condition, 'left pursuit' participants engaged in sinusoidal pursuit with amplitude of ±5º and a frequency of 0.5 Hz, except this time the pursuit cycle starts at -7.5º eccentricity.

The experiment comprised of a boxcar design, with 15 x 60 second epochs consisting of a 10s central fixation baseline period immediately followed by the 10s 'central pursuit' condition (active period), then a 10s right fixation period, 10s 'right pursuit' condition, 10s left field fixation and finally 10s of 'left pursuit'. Each run lasted for about 15 minutes.

Apparatus and data acquisition

Visual stimuli were generated on a GeForce graphics card (Nvidia Corp.) and back-projected (Sanyo XP41 LCD) onto a screen at 60 Hz (size 34 x 24.7 cm, total visual angle 25.6 x 19.2 degrees, resolution of 1024 x 768) at a distance of 71 cm. The visual stimuli and experimental protocol were programmed in Pascal (Delphi 7, Borland Software Corporation) using the OpenGL software library for graphics hardware.

MEG data was recorded using a 275 channel whole-head system (CTF Systems Inc., a subsidiary of VSM MedTech Ltd.) in a magnetically-shielded room at a sample rate of 1.2 kHz using a radial gradiometer configuration, with the primary sensors analysed as synthetic

third order gradiometers. During data acquisition, head position and motion were monitored using 3 fiduciary markers placed on the nasion and 1 cm anteriorly from both the left and right tragi. Each participant's MEG data was then co-registered with their anatomical data, based on the position of these easily identifiable anatomical landmarks from the MR scan. These points were verified using high-resolution digital photographs taken during fiducial placement.

Electrooculographic (EOG) recordings were taken at the same time as MEG data collection, which allowed us to characterise eye movements while observers wore polarizing goggles designed to eliminate any retinal illumination other than from the faintly visible pursuit target. Pairs of electrodes were placed above and below the eye to record vertical displacement, and to the lateral corner of each eye to record horizontal displacement. The impedance of each electrode was then measured to ensure satisfactory conductance of the EOG signal. Skin preparation was performed again and the electrodes were re-applied if the electrical resistance was found to be above a pre-defined threshold of 5 kΩ.

Data analysis

For localisation of the oscillatory response, a multiple, local-spheres forward-model was derived by fitting overlapping spheres (Huang, Mosher, & Leahy, 1999) to the brain surface extracted by the Brain Extraction Tool (BET) (Smith, 2002). Source analysis was performed using Synthetic Aperture Magnetometry (SAM), a non-linear beamformer spatial filter that generates statistical parametric maps of oscillatory power changes (Pfurtscheller & Silva, 1999) between baseline/passive (fixation) and active (stimulus tracking/retinal motion) periods within specific frequency bands.

SAM images were constructed on a 5x5x5 mm grid throughout the brain for each condition and each participant. Oscillatory changes between the passive and active periods for all 30 epochs were mapped for alpha (5-15 Hz), beta (15-25 Hz) and gamma (30-80 Hz) frequency ranges. Peak coordinates for activation in the specified frequency band in the SAM images were visualised using mri3dX (Singh, 2009) and chosen on the basis of their locality within extra-striate cortex, for peaks with a predefined threshold of pseudo-t values greater than 0.5 and with an exclusion radius of 5 mm. These coordinates were used to compute suitable weights for virtual electrode generation on an individual basis and used in all subsequent analyses (performed using custom-scripts in Matlab). Virtual sensor weights were estimated using a covariance matrix filtered between 15-25 Hz (hence, modulations seen in this spectrogram can only be guaranteed to be coming from the desired location for this

frequency range). Computation of these time-frequency spectrograms were performed at peak voxel locations based on the Hilbert transform, in 0.5 Hz steps. The percentage change in oscillatory amplitude during the active period was baselined against the 0-10 second passive period.

Experiment 2

Participants

Twenty participants with normal or correct-to-normal visual acuity completed Experiment 2 (12 females, mean age = 22.3 yrs). All participants had given prior informed consent and no history of neurological disorders. All experimental procedures were approved by the Cardiff University School of Psychology Ethics Committee.

Design and procedure

Figure 2 here

Figure 2 depicts the protocol for Experiment 2. Participants begin by fixating a central point (baseline period, 3 seconds). This was followed by the appearance of a target in the right hemifield at 12.5º eccentricity, which observers were instructed to make an immediate eye movement towards and then fixate. After 3 seconds, this target stimulus then moved leftwards at either -5, -10 or -15º/s for 25º of visual angle. This period is then immediately followed by another central fixation (3s), which in turn is followed by a left field fixation (amplitude -12.5º, gaze held for 3s). A period of rightwards smooth pursuit at 5, 10 or 15º/s for 25º then follows. Thus, there were six conditions in total, each comprising of pursuit along the horizontal meridian, with 15 trials of each velocity. Condition presentation was randomised and counter-balanced within the whole run.

Data analysis

SAM images were constructed for each velocity versus the central fixation baseline period. The percentage change in the amplitude for pursuit was referenced to the baseline fixation period. Alpha and beta amplitude changes relative to baseline was sampled over a 1 second time window during the central portion of the pursuit phase for use in later analyses. By sampling amplitude changes partway through the pursuit phase, smooth pursuit gain was likely to be closer to 1, thus reducing the likelihood that any measured changes in alpha and beta amplitude would be related to significant retinal slip or catch-up saccades. To further ensure this was the case, any trials that were found to be severely contaminated with saccadic

7

eye movements, or blinks, were removed from any further imaging analysis, resulting in an average trial exclusion rate of 13.3% per participant per session.

Results

Experiment 1

Eye movement data

<div align="center">

Figure 3 here

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Figure 3 shows the group mean pursuit gain. Visual inspection of the EOG traces revealed that observers were able to track the moving stimulus reasonably accurately. This was confirmed by the group mean pursuit gains shown in Figure 3. Crucially, a repeated measures ANOVA revealed no significant difference between the mean gains found in the 3 pursuit conditions ($F(2,17) = 1.722$, $p > 0.05$).

SAM source analysis

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Figure 4 here

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Figure 4a shows the group mean SAM analysis for 15-25 Hz activity. This revealed bilateral extra-striate suppression of the beta response for the 'central pursuit' versus baseline central fixation condition in all participants. As this frequency band displayed the most consistent peaks localised to putative MT+ (similarly to Dunkley et al., 2013), these coordinates were used to compute the weights required for the virtual sensors (over a 0.1 to 80 Hz range), and the subsequent time-frequency analysis using the Hilbert transfer (in 0.5 Hz steps). Additionally, areas of the PPC, FEF and cuneus showed evidence of beta rhythm amplitude decreases. The group average beta response with a peak in left association cortex is indicative of the individual source localisation results. Furthermore, alpha changes for central pursuit eye movements were, for the most part, spatially coincident with the beta response shown above; that is, located in association cortex consistent with MT+, PPC, FEF and cuneus. However, the beamformer reconstruction of the beta rhythm proved to be more reliable in its estimation of MT+. Finally, there were no gamma (30-70 Hz) responses evident in any individual or Group SAM images.

Time-frequency analysis

Figure 4b shows the group-averaged spectrogram from the virtual electrode in left MT+ during eye movement for all three pursuit eccentricities. Trials began with the central fixation baseline window, which was then followed by the 'central pursuit' condition, right fixation, 'right pursuit' condition, left fixation and finally 'left pursuit'. The time-frequency analysis from left MT+ revealed sustained, low frequency (5-25 Hz) amplitude decreases for the duration of tracking for all three conditions. A similar response profile alpha-beta changes

was also observed in right MT+, with sustained suppression for the duration of all three conditions. There is no evidence in the spectrograms of any discernable difference in the alpha or beta response as a function of pursuit cycle eccentricity.

Additionally, there appears to be demarcation in the oscillatory amplitude changes of the 5-25 Hz frequency band (denoted by the white bounded box in the spectrograms of Figure 4b), showing sustained amplitude decreases in two distinct frequency bands during pursuit eye movements in MT+. One of these is in the range of the alpha band, and the other in the higher beta band. The pattern of these responses is similar to those found in our previous paper (Dunkley, et al., 2011). This effect appeared more prominent in the left MT+ voxel (right MT+ time course not shown for brevity).

To assess the spectral characteristics of these pursuit-related responses, Amplitude versus Frequency plots were computed from the averaged, active time-windows and all participants (**Figure 4c**). These revealed two peaks; the largest peak being around the 5-15 Hz band, and a second, smaller, peak at around 18-22 Hz (approximately beta frequency). On this basis, the broadband 5-25 Hz signal was decomposed into two smaller frequencies for further analysis. These 5-15 and 15-25 Hz amplitude envelopes from MT+ were examined for differences in the modulation of this activity at the three pursuit eccentricities. This was then compared across conditions during the sinusoidal pursuit cycle, discussed in the next section.

Oscillatory amplitude envelope analysis

Figure 5 here

Figure 5 shows the group-averaged amplitude envelopes in the alpha (*top panels*) and beta bands (*bottom panels*) relative to the baseline central fixation condition, in both left and right MT+ during a pursuit cycle. For reference, the dashed line in each figure shows the phase of the relative eye position during each cycle (the eye position units are arbitrary). Different colours denote the three different eccentricities (centre, left and right).For both alpha and beta responses, amplitude appears to be independent of eccentricity throughout the pursuit cycle. The modulation of low-frequency oscillations in MT+ shows no evidence of ipsi- or contralateral eye position-dependence (relative to the MT+ recording site).

There does appear to be a consistent modulation of the alpha and beta amplitude envelope within the pursuit cycle. In the left MT+ recording site, alpha and beta seems to covary with eye position in the contraversive phase of the pursuit cycle. Hence, there is a salient trough in the first half of the pursuit cycle, when the eyes are moving away from the

left recording site, but this then flattens in the second half of the cycle. For right MT+ however, the shape resembles more of a symmetrical 'W' shape, with two minima in the alpha and beta amplitude corresponding to the maximum amplitude of the eyes during the pursuit cycle. Therefore, it is possible these amplitude envelope profiles could reflect a process that reflects either eye speed or direction, which was the motivation of Experiment 2.

Experiment 2

Eye movement data

Figure 6 here

Figure 6a shows the group-averaged horizontal eye position trace when tracking the stimulus in both the left- and rightwards directions and the mean pursuit gain for each condition (note the eye movements were analysed over the middle 1-second window during tracking of the stimulus). Participants with mean gain values not falling within the predefined range of 0.8 to 1.2 across all conditions were excluded from further behavioural and imaging analysis, in order to minimise the amount of retinal slip affecting subsequent analyses. This resulted in the exclusion of one participant whose average gain value was 0.78, leaving a cohort of 19 participants.

One-Way ANOVA on eye velocity gains for leftwards and rightwards pursuit direction revealed no significant difference in velocity for leftwards ($F(2,36) = 0.30$, $p > 0.05$) or rightwards pursuit ($F(2,36) = 0.20$, $p > 0.05$). However, when mean pursuit gain was collapsed across conditions to give a mean measure of pursuit gain based on directionality, there was a significant if small difference in the mean eye velocity gain for left- versus rightwards pursuit (paired t-test, $t(56) = -2.62$, $p < 0.05$). .

SAM source reconstruction

Figure 7 here

Figure 7a shows a representative single-subject SAM analysis for beta during stimulus tracking at -10º/s, versus the central fixation baseline period. This revealed bilateral 15-25 Hz suppression over extra-striate cortices, consistent with MT+, in addition to peaks over the FEF, SEF, and PPC regions. Similar patterns of activity to this were observed for this subject in the alpha band for all other pursuit velocities in both the left- and rightwards directions. No gamma peaks were identified in any of the participants in the MT+ region. The beta response observed during pursuit, as in previous experiments, was shown to be the most consistent in the SAM source estimation for localising MT+ for the majority of subjects.

11

Therefore, the location of this beta band peak response was used it was used to define the coordinates for the virtual sensor reconstruction at 0.1-80 Hz, and subsequent time-frequency analysis using the Hilbert transform.

Time-frequency analysis

Grand-averaged time-frequency plots of the oscillatory changes in right MT+ for leftwards pursuit can be seen in **Figure 7b**. Both the left- and rightwards direction induced sustained low-frequency (5-25 Hz) suppression for the duration of object tracking starting 0 seconds onwards. Interestingly, there was also consistent suppression of the 5-25 Hz response in MT+ when the eyes are fixated and stationary in the right visual hemifield following saccadic eye movements to the eccentric fixation point.

In the central fixation baseline period (the time window -6 to -3 seconds denoted by CF), there is 1-2 seconds of low-frequency suppression proceeding termination of pursuit and the subsequent saccade to the central fixation point. This appears prominent in the alpha band, with a greater decrease in amplitude and often sustained for longer than the suppression in beta. Following this, alpha and beta amplitude returns to baseline levels after 1-2 seconds.

Following the time-frequency analysis, the mean alpha and beta activity in the central one second time window of the pursuit phase was extracted from each individual's spectral data and used to examine pursuit velocity modulation activity from this region (denoted by the white box in the spectrograms).

Effect of eye velocity on low-frequency suppression

Figure 8 here

Figure 8a depicts the mean alpha response for each stimulus velocity in left (top row of panels) and right (bottom row) MT+. A One-way Repeated Measures ANOVA was run for each hemisphere and pursuit direction separately. Results indicated there was no significant effect of stimulus velocity on alpha (all ANOVA tests $p > 0.05$).

Figure 8b shows the mean beta amplitude for each of the stimulus velocity conditions, in both the leftwards and rightwards direction, in left and right MT+. For beta amplitude change from the left hemisphere during leftwards pursuit (top left panel), there was no significant difference in the mean induced beta response ($p > 0.05$). There was a significant effect of stimulus velocity on the beta amplitude measured from the left hemisphere during rightwards pursuit (top right panel, $F(2,32) = 4.39$, $p < 0.05$), as well as a significant effect of stimulus velocity on beta for leftwards pursuit in the right hemisphere

12

(bottom left panel, $F(2,32) = 6.74$, $p < 0.01$). Finally, for beta from right MT+ during rightwards pursuit (bottom right panel), there was a significant effect of stimulus velocity on the magnitude of the beta amplitude change in MT+ ($F(2,31) = 3.862$, $p < 0.05$).

In summary, although we did not find *direction*-specific changes in the response as originally predicted, there does however appear to be a trend for increased beta suppression with increasing eye *speed*, irrespective of the direction of the pursuit eye movement. This would suggest that beta amplitude decreases might be linked to activity in these regions that is related to the processing of oculomotor and/or extraretinal eye movement signals coding for eye speed. A further set of analyses was therefore performed to compare alpha and beta activity with changes in eye speed. This was achieved by simply reversing the sign of the leftwards stimulus velocity and collapsing the left- and rightwards data together, resulting in 4 tests (for both alpha and beta responses, and each hemisphere). The results of this analysis are discussed in the next section.

Effect of eye speed on low-frequency suppression

Figure 9 here

Figure 9 shows the mean alpha (top panels) and the beta (bottom panels) activity for each eye speed condition, from both the left and right MT+. Repeated-measured ANOVA for the alpha found there was no significant effect of eye speed on amplitude in either the left or right hemispheres (top panels, $p > 0.05$).

There was a significant effect of eye speed on beta in the left hemisphere (bottom left panel, $F(2,65) = 4.73$, $p = 0.01$)). Post-hoc comparisons found beta suppression in the 15º/s ($M = -10.15$, $SD = 7.95$) condition was significantly greater than the 5º/s ($M = -14.60$, $SD = 7.61$) condition ($p = 0.015$).

For the right hemisphere MT+ beta, there was a significant effect of eye speed on the amplitude ($F(2,65) = 10.65$, $p < 0.001$), with post-hoc comparisons indicating a significant difference between the 5º/s ($M = -11.84$, $SD = 8.69$) and 15º/s ($M = -19.29$, $SD = 12.87$) conditions ($p < 0.001$). Additionally, there was also a significant difference between the 10º/s ($M = -14.27$, $SD = 9.57$) and 15º/s ($M = -19.29$, $SD = 12.87$) conditions ($p = 0.012$), but not for the other conditions ($p > 0.05$). Therefore, this might suggest some functional distinction in the role of alpha and beta suppression in MT+ during pursuit.

13

Discussion

Two experiments were carried out to further explore the link between oscillatory suppression in MT+ and smooth pursuit eye movement (Dunkley et al, 2013). In Experiment 1, we investigated whether the modulation reflects head –centred eye position or velocity. In Experiment 2, we tested whether modulation was related to the speed or direction of the eye movement.

The results of Experiment 1 showed that the alpha and beta amplitude envelopes measured during pursuit showed no differential response related to eye position. Activity was virtually identical across the three eccentricities tested, suggesting that responses from MT+ during eye movements reflect the activity of neurons that code for some other aspect of pursuit, such as eye speed. In Experiment 2, we found little connection between alpha and beta activity, and the direction of pursuit (although there was a trend for slightly greater suppression for contraversive eye movements). However, we did find a significant effect of *eye speed* on beta suppression, whereas there was no similar effect on alpha. This suggests that beta suppression represents a distinct mechanism related to pursuit behaviour, reflecting some fundamental aspect of the eye movement, while alpha suppression does not. We speculate that the latter is more likely to reflect the hypothesised 'inhibitory gating' mechanism (Handel, Haarmeier, & Jensen, 2011; Jensen & Mazaheri, 2010), or perhaps superordinate functions such as visuo-spatial attention that have been implicated in intentional pursuit eye movements (Lovejoy, Fowler, & Krauzlis, 2009; Ono & Mustari, 2006).

The beta suppression we found could be related to neuronal activity involved in oculomotor control (Ilg et al., 1997; Krauzlis, et al., 2004) or it could be related to the integration of extraretinal information in the perception of motion during pursuit (Freeman, Champion & Warren 2010; Spering & Montagnini, 2011; Furman & Gur). It is not possible to draw a definitive conclusion from this experiment on either of these issues, as this task was performed in the presence of visual feedback in the form of the retinal slip that accompanies closed-loop pursuit. Given this, it is not possible to isolate purely 'extraretinal' components of a reference signal without looking at pursuit activity in absence of any visual input (thereby fully isolating nonretinal mechanisms). Additionally, without an objective measure of perceived motion during pursuit, it is also not possible to conclude whether alpha and beta oscillations are used in this process either. However, this experiment does suggest a fundamental role of beta suppression in MT+ during ongoing pursuit, whether it be in the

14

generation of oculomotor signals or the integration of an internally generated reference signal that codes eye speed estimates.

It has been shown that alpha and beta decreases in striate and association cortices might reflect the engagement of visuo-spatial attention and anticipatory processing of any predictable sensory change and incoming information (Worden, Foxe, Wang, & Simpson, 2000; Yamagishia, Callana, Anderson, & Kawatob, 2008). In other words, alpha and beta amplitude decreases occur over the area of cortex known to be active when covert visuo-spatial attention mechanisms are engaged, and this effect is enhanced in this region of the brain by anticipatory signals awaiting an impending sensory change). It is possible the sustained alpha and beta suppression witnessed during gaze fixation reflects an "inhibitory filter mechanism" (Jensen & Mazaheri, 2010) that helps focus attention (or perhaps attention itself modulates this change; causality cannot be implied in this case) and prevents distracting stimuli from interfering with task-related processing, given that the onset of the motion stimulus can be anticipated. Therefore, it seems likely that the oscillatory response observed in MT+ during excursive gaze fixation could represent either the allocation of selective visuo-spatial attention and anticipatory priming of the brain for stimulus motion onset, the macroscopic signature of neuronal activity reflecting eye position sensitivity, or a combination of both these processes.

In Experiment 2, this was examined by utilising a paradigm similar to that used in other studies (Ilg & Thier, 2003; Nagel, et al., 2008), to test whether the neuronal response characteristics, defined as oscillatory amplitude changes, reflect a velocity-based signal. Additionally, the data was examined further to see whether a response for a preferred direction could be extracted from the macroscopic signature, given that animal research suggests the majority of neurons in MST that display a pursuit-related response code for ipsiversive pursuit (Ilg & Thier, 2003).

Consistent beta suppression was found over extra-striate cortices for all stimulus conditions and a significant effect of pursuit eye speed on the magnitude of the beta decreases (increased suppression with increasing eye speed). Furthermore, no effect of eye speed on alpha in MT+ was found. This suggests there might be some functionally distinct role that these frequency bands play in the maintenance of pursuit and/or the integration of extraretinal eye movement signals in this area.

The findings presented here do not conform to our original predictions regarding a speed-sensitive bias in alpha and beta suppression for ipsiversive pursuit directionality (relative to

15

the recording site). Given these results, we speculate that the relationship between beta suppression and eye speed demonstrates functionally relevant role with regards to smooth pursuit. Specifically, it appears that the brain may engage in active beta band suppression in MT+ during pursuit, which could either reflect the generation of oculomotor signals for pursuit maintenance in the presence of ongoing visual feedback and/or the use of extraretinal signals for perceived motion during pursuit. The lack of any clear relationship between alpha activity and the eye movement also suggests that suppression mediates, or is perhaps in turn mediated by, some other sensory or cognitive process associated with pursuit.

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Figure captions

Figure 1. Experimental protocol for the excursive pursuit paradigm (Experiment 1). Sinusoidal pursuit eye movements were performed at three horizontal eccentricities (central, right and left hemifield) in the sequence shown.

Figure 2. Experimental protocol for the pursuit velocity experiment (Experiment 2). Participants fixate a central stimulus for 3 seconds (baseline condition), followed by either a fixation to the left or right at -12.5° or 12.5° respectively. Active tracking then followed where participants pursue the target stimulus at one of three speeds (5, 10 or 15°/s) in either direction, given six total velocities (3 levels per factor).

Figure 3. Group-averaged pursuit gains values for the three eccentricities examined. Error bars are ±1SE throughout.

Figure 4. (a) Group-averaged SAM images for beta overlaid on a template brain. Cold-colour map indicates task-induced amplitude decreases, with the greatest changes localised to bilateral extra-striate regions. **(b)** Group averaged spectrogram for left MT+. Low-frequency suppression (5-25 Hz decreases, delineated by the white-bounded box) was observed for all three pursuit conditions as denoted by the cold-colour map (indicating percentage change from baseline). **(c)** Group-mean spectral power from left and right MT+ during pursuit phase. Normalised absolute amplitude changes in frequency show a peak at around 5-15 Hz, and a second, smaller peak at around 18-22 Hz, consistent with the alpha and beta bands, respectively.

Figure 5. Group-averaged amplitude envelopes for alpha (top row) and beta (bottom row). A representative sinusoidal pursuit cycle showing the relative phase of the ongoing eye movement is denoted by the dashed grey line (arbitrary units). The 'central pursuit' condition is depicted by the red trace, 'right pursuit' condition in green, and the 'left pursuit' condition in blue. Shaded regions define ± 1SE. The percentage amplitude changes shown are all relative to the baseline central fixation period.
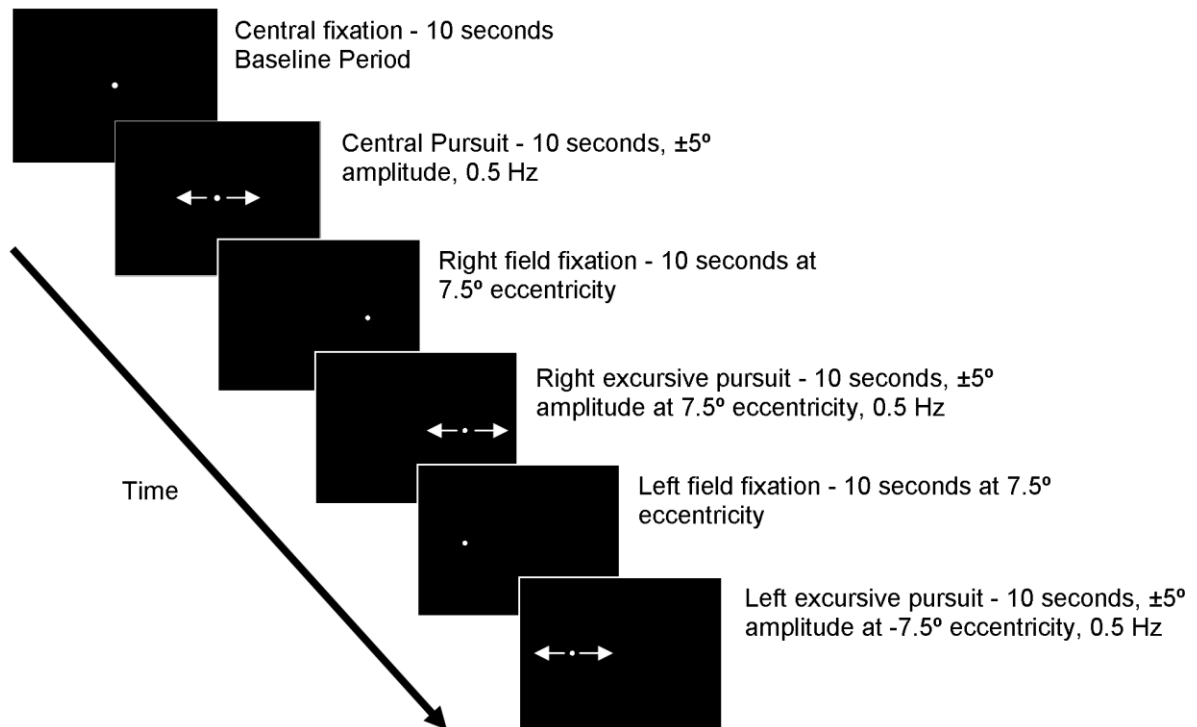
Figure 6. (a) Group-averaged horizontal eye position traces for pursuit in both the leftwards (left panel) and rightwards (right panel) direction. **(b)** Group mean pursuit gain for leftwards (left panel) and rightwards (right panel) eye movements conditions. Gain was calculated over the central 1 second window midway through the pursuit eye movement.. **(c)** Group mean pursuit gain, collapsed across all velocity conditions, for both the left and rightwards direction. Error bars are $\pm$1SE throughout. (*p < 0.05).

Figure 7. Single-subject SAM analysis for beta during leftwards pursuit at -10º/s and group-averaged spectrograms for right MT+. **(a)** SAM analysis revealed beta decreases over right extra-striate cortex, consistent with MT+, along with a second peak identified in left MT+. Additionally, there were peaks identified in FEF, SEF, the cerebellum and the PPC. **(b)** Grand-averaged spectrograms from right MT+ during leftwards pursuit. The baseline period (central fixation: CF) was followed by right field fixation (RF) at 12.5º from -3 to 0 secs. Subsequently, there was leftwards pursuit (LP) at either -5, -10, -15 or -20º/s, terminating at -12.5º eccentricity. White box denotes the time-period over which the average amplitude change was quantified and subsequently used when examining speed modulation of alpha and beta in MT+.

Figure 8. (a) Mean alpha responses from both left and right MT+ for each of the speed conditions in the leftward and rightward pursuit directions. Negative amplitude values indicate a decrease with respect to baseline. **(b)** Mean beta responses. Error bars are $\pm$SE throughout. (* = p < 0.05, ** = p < 0.01).

Figure 9. Mean magnitude of alpha and beta suppression in both the left and right hemispheres at various pursuit speeds Error bars are $\pm$SE throughout . (* = p < 0.05, ** = p < 0.01).
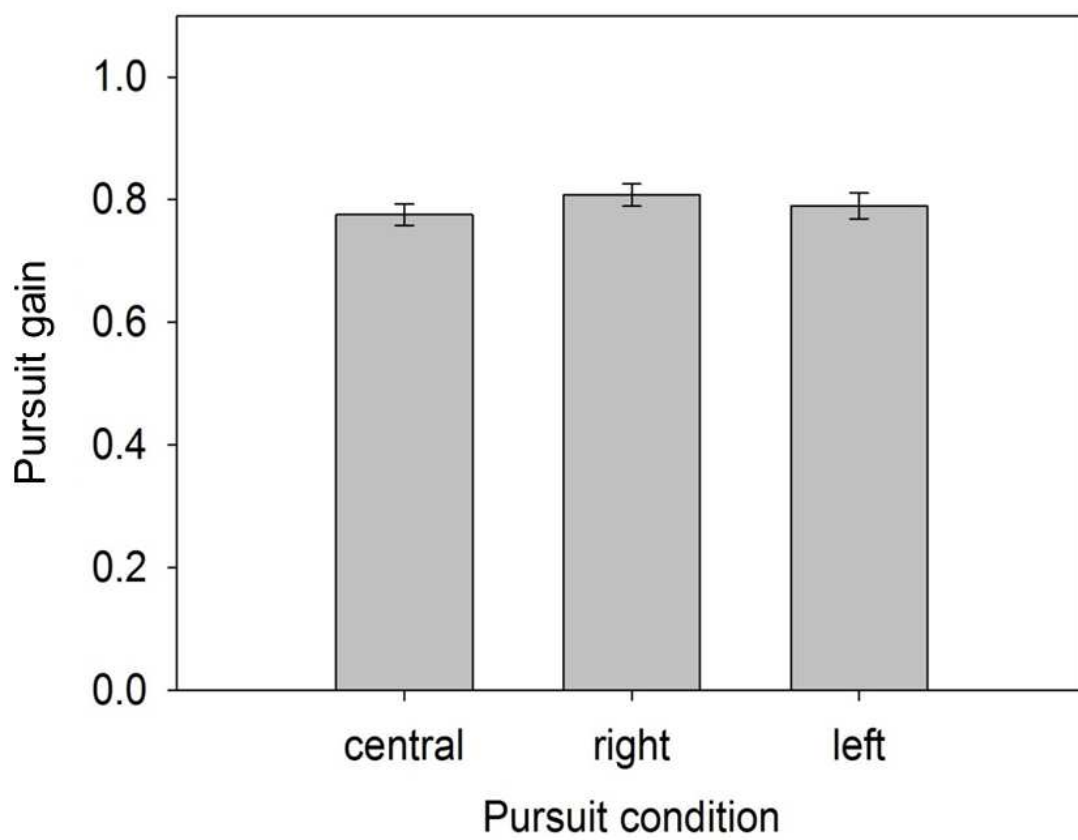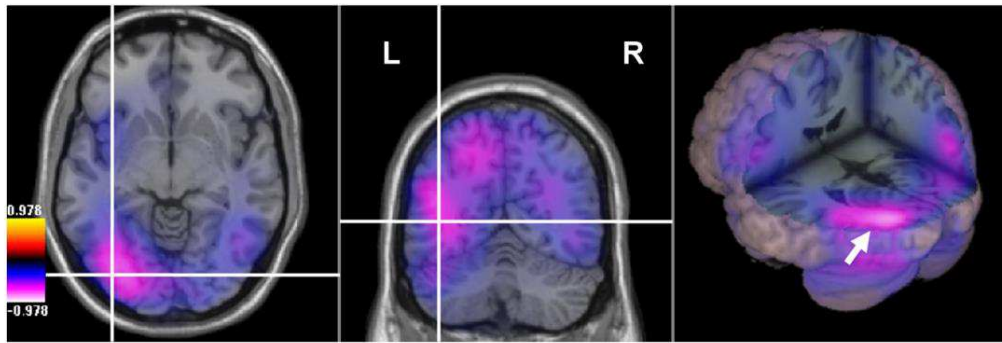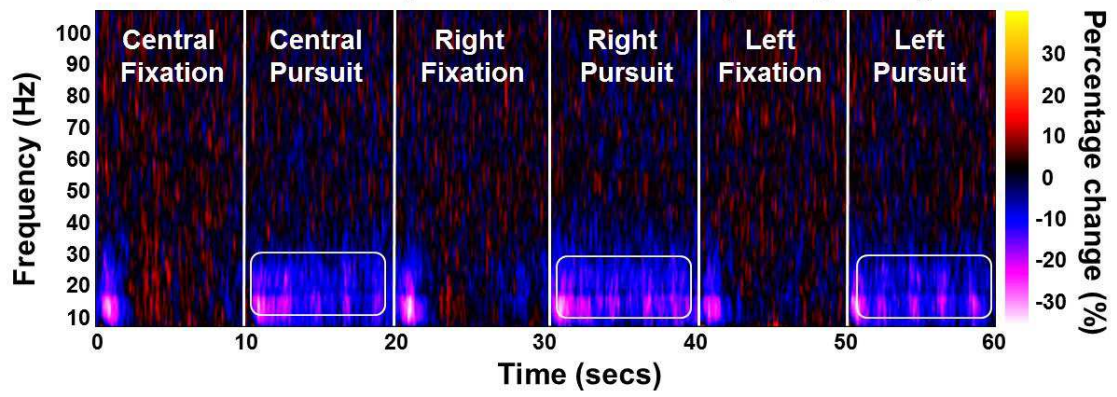
Figures

Central fixation - 10 seconds
Baseline Period

Central Pursuit - 10 seconds, ±5º
amplitude, 0.5 Hz

Right field fixation - 10 seconds at
7.5º eccentricity

Right excursive pursuit - 10 seconds, ±5º
amplitude at 7.5º eccentricity, 0.5 Hz

Left field fixation - 10 seconds at 7.5º
eccentricity

Left excursive pursuit - 10 seconds, ±5º
amplitude at -7.5º eccentricity, 0.5 Hz

Time

Central fixation - 3 seconds
Baseline Period

Right field fixation - 3 seconds at
12.5 degs eccentricity

Leftwards pursuit - 5, 10 or 15 deg/s,
terminating at -12.5 degs

Central fixation - 3 seconds
Baseline Period

Left field fixation - 3 seconds at -12.5
degs eccentricity

Rightwards pursuit - -5, -10 or -15 degs/s,
terminating at 12.5 degs

Time

Pursuit tracking gain

a

Group SAM analysis - 15-25 Hz suppression

b

Left hemisphere MT+ time-frequency analysis

c

Alpha (5-15 Hz) response

Left hemisphere MT+ alpha envelope analysis

Right hemisphere MT+ alpha envelope analysis

Beta (15-25 Hz) response

Left hemisphere MT+ beta envelope analysis

Right hemisphere MT+ beta envelope analysis

a Leftwards pursuit — Rightwards pursuit

b Pursuit gain

c Effect of pursuit directionality on gain

27
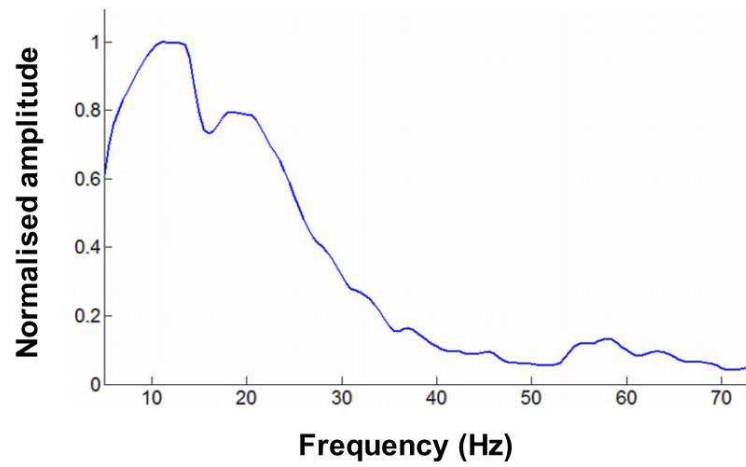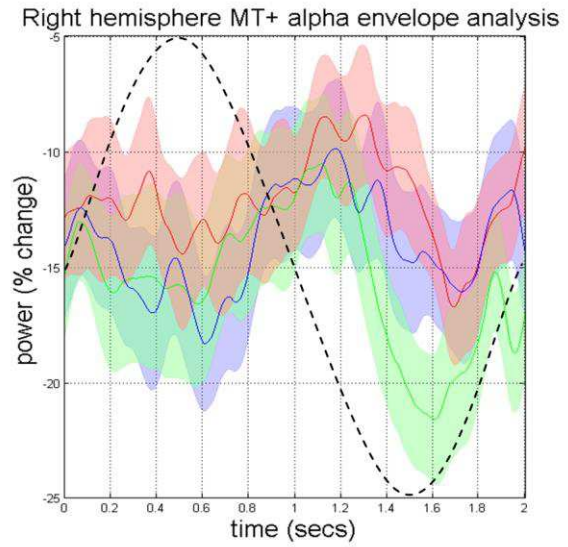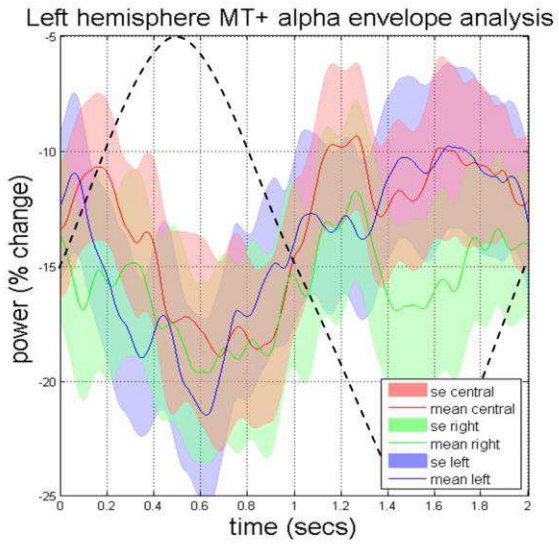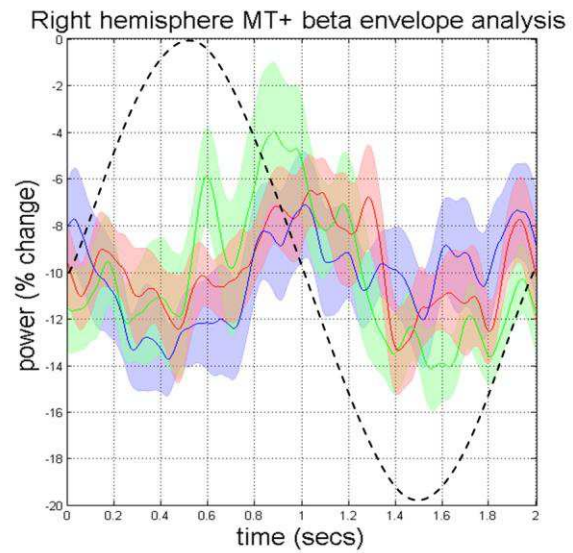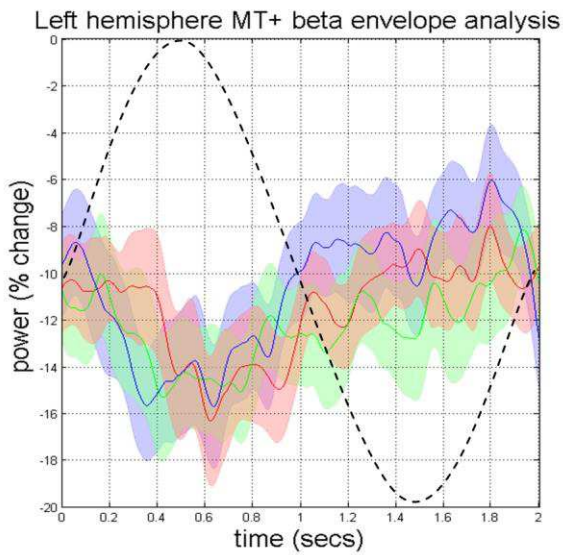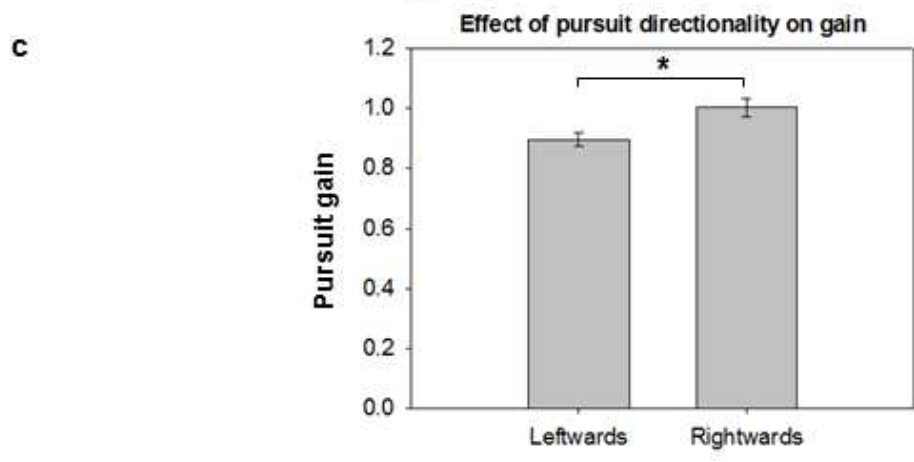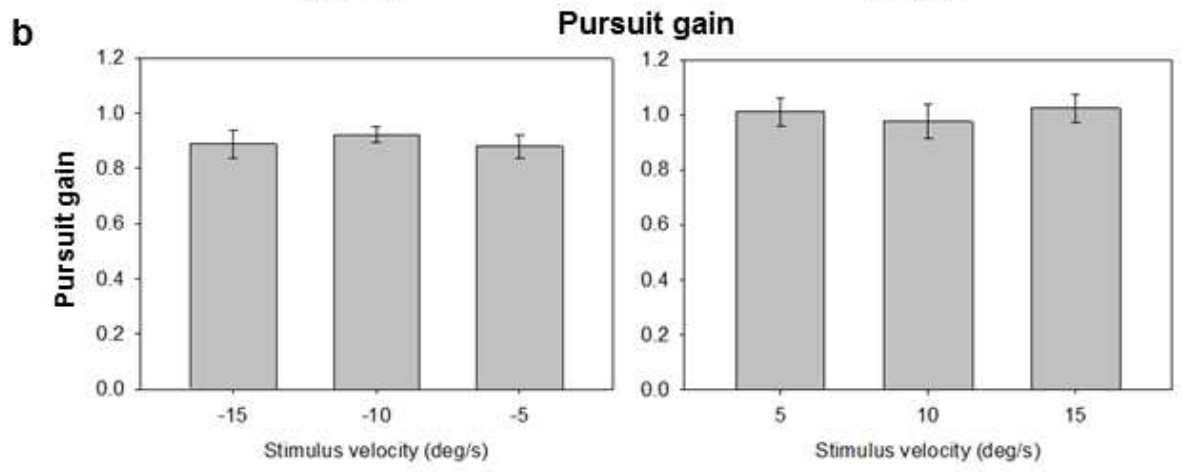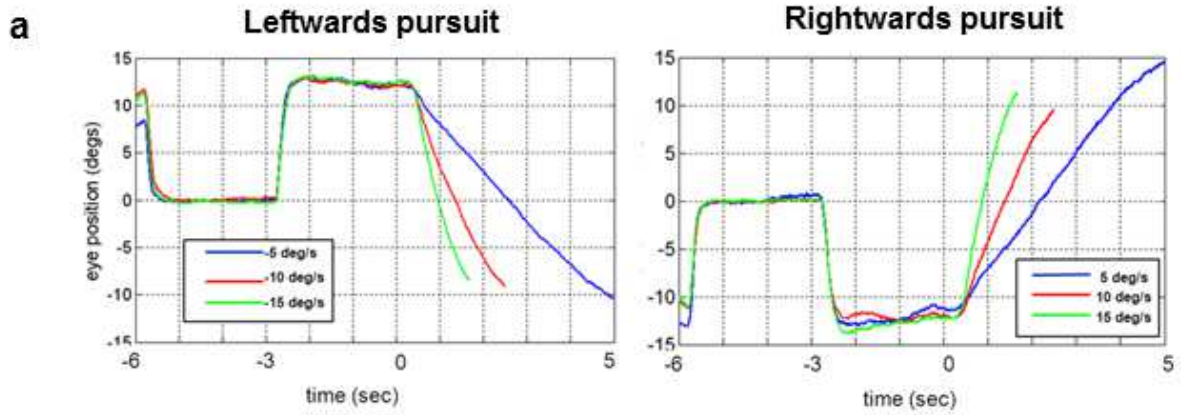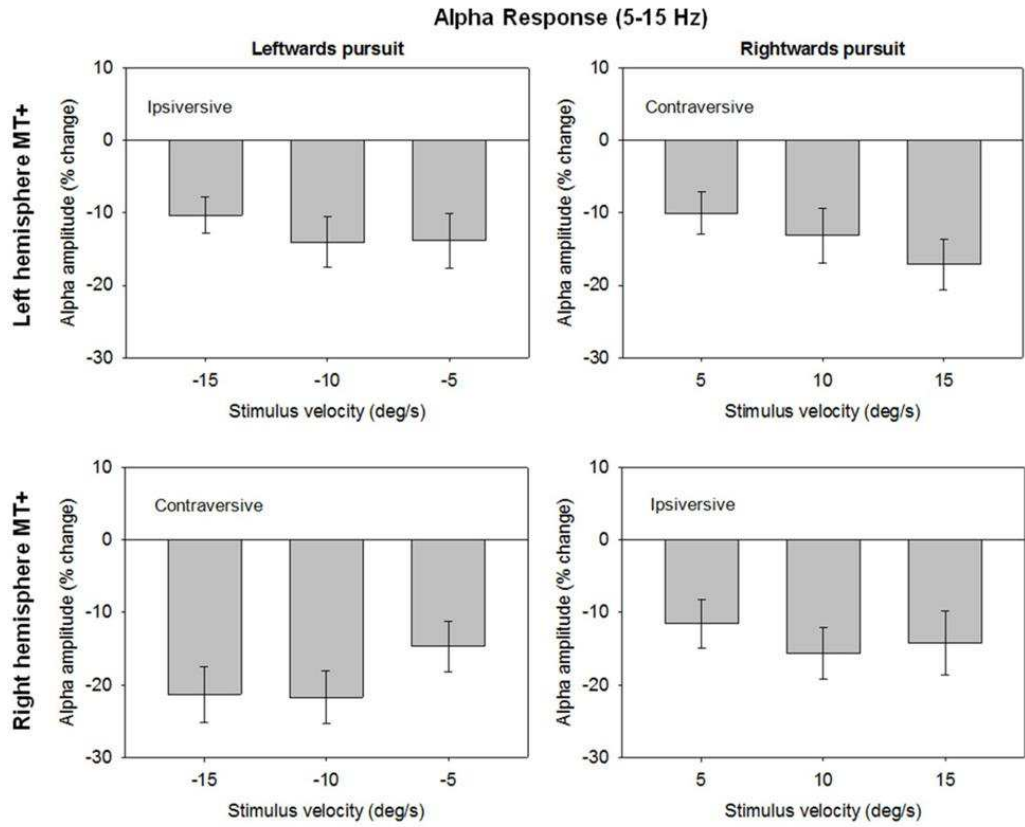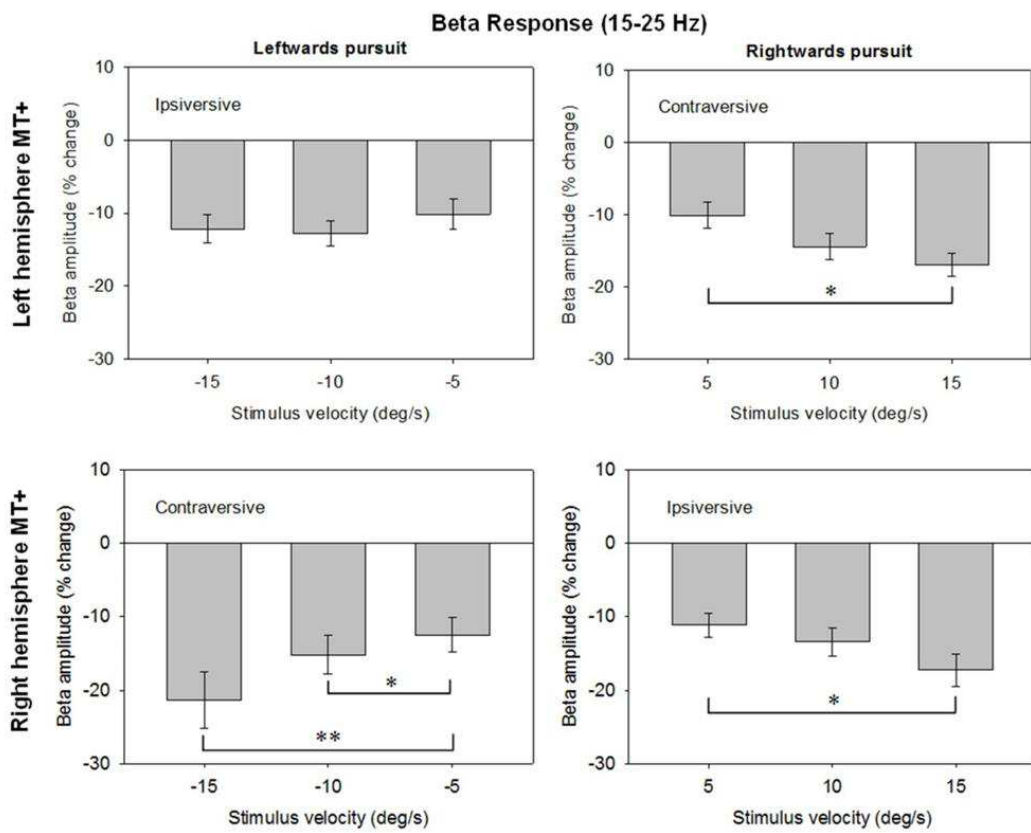
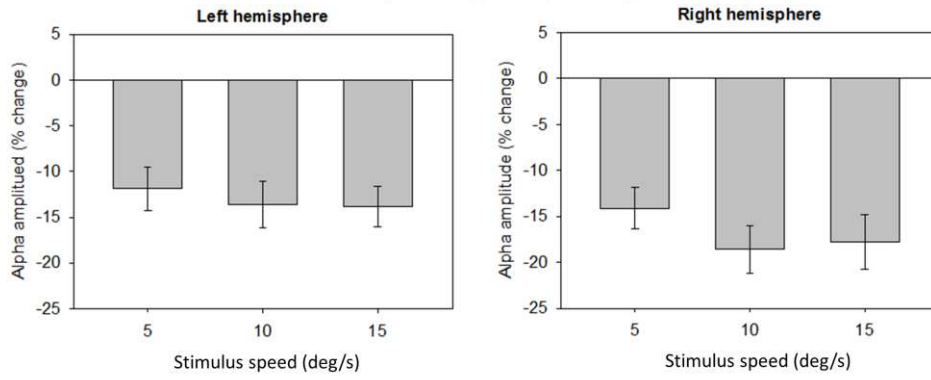**Single-subject SAM analysis -15-25 Hz suppression**
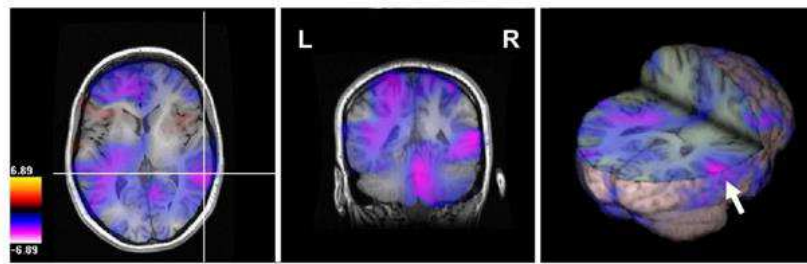
Right hemisphere - Leftwards pursuit time-frequency analysis

28

a Alpha Response (5-15 Hz)

b Beta Response (15-25 Hz)

Alpha Response (5-15 Hz)

Left hemisphere — Right hemisphere

Beta Response (15-25 Hz)