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Processing of gaze direction within the N170 / M170 time window: A combined EEG / MEG study.

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ABSTRACT

Gaze direction is an important social signal for human beings. Beside the role of gaze in attention orienting, direct gaze (that is, gaze directed toward an observer) is a highly relevant biological stimulus that elicits attention capture and increases face encoding. Brain imaging studies have emphasized the role of the superior temporal

sulcus (STS) in the coding of gaze direction and in the integration of gaze and head cues of social attention. The dynamics of the processing and integration of these cues remains, however, unclear. In order to address this question, we used deviated and frontal faces with averted and direct gaze in a combined electro- and magneto-encephalography (EEG–MEG) study. We showed distinct effects of gaze direction on the N170 and M170 responses. There was an interaction between gaze direction and head orientation between 134 and 162 ms in MEG and a main effect of gaze direction between 171 and 186 ms in EEG. These effects involved the posterior and anterior regions of the STS respectively. Both effects also emphasized the sensitivity to direct gaze. These data highlight the central role of the STS in gaze processing.

KEYWORDS: GAZE DIRECTION; MEG; EEG; M170; N170

1. INTRODUCTION

Among all the facial signals that are essential to social cognition, the direction of gaze appears to be a particularly important cue in many ways. Gaze direction indicates the direction of one's attention and focus of interest in the surrounding space. For instance, direct gaze indicates attention directed at the observer, constituting the most primary form of social contact and a frequent preliminary to interindividual interactions (for a review, see George & Conty, 2008). Direct gaze has been shown to capture attention (Conty, Tijus, Hugueville, Coelho, & George, 2006; Senju & Hasegawa, 2005; Stein, Senju, Peelen, & Sterzer, 2011; von Griinau & Anston, 1995). It also seems to induce deepened or enhanced encoding of the seen face, leading to better memory for faces with direct than averted gaze—particularly when they are presented under a deviated head view, at the behavioural level (Macrae, Hood, Milne, Rowe, & Mason, 2002; Vuilleumier, George, Lister, Armony, &

Driver, 2005, see also George, Driver, & Dolan, 2001). On the other hand, averted gaze perception can elicit an automatic shift of the observer's spatial attention in the direction of the seen gaze, leading to the so-called gaze cueing effect – faster detection and recognition of targets falling under the gaze of another person as compared to not-gazed-at targets (Driver et al., 1999; Friesen & Kingstone, 1998). Thus, the processing of gaze direction is essential in social interaction.

One aspect of gaze direction perception and of the coding of the direction of others' attention concerns the integration between gaze direction and head orientation cues. Both gaze direction and head orientation are cues to the direction of another person's attention. Perrett et al. (1992) have proposed a hierarchical processing of these cues with gaze processed first and dominating over head orientation, which in turn dominates over other cues such as body orientation. However, while some behavioural studies in humans confirmed gaze as a predominant cue to the direction of others' attention (Driver et al., 1999; Frischen, Bayliss, & Tipper, 2007), other studies indicated reciprocal influences in the processing of gaze and head cues (Itier, Alain, Kovacevic, & McIntosh, 2007; Langton, 2000; Langton & Bruce, 1999). Moreover, the timecourse of the cerebral integration of gaze and head cues to the direction of others' attention remains unclear.

Both gaze direction and head orientation constitute variant features of faces. It has been argued that the coding of such variant, fundamentally dynamic features would involve lateral temporal cortex regions centred on the superior temporal sulcus (STS) (Bernstein & Yovel, 2015; Haxby, Hoffman, & Gobbini, 2000; Hoffman & Haxby, 2000; Ishai, 2008). However, it is unclear if these variable cues are subject to early integration during the perceptual analysis of faces. Moreover, while many

studies examined the integration of gaze and emotional facial expression (using frontal views of faces only) (e.g., Klucharev & Sams, 2004; Rigato et al., 2010; Ulloa et al., 2014; for review, Graham & Labar, 2012), the question of the cerebral dynamics of the processing of gaze and head cues to the direction of others' attention—with neutral faces—has received less attention. Previous studies with electroencephalography (EEG) or magnetoencephalography (MEG) have shown early processing of gaze direction in the form of modulations of the so-called N170 (in EEG) and M170 (in MEG) in response to faces. The N170 and M170 are components of the event-related potential (ERP) and event-related magnetic field (ERF) respectively, selective for face perceptual analysis, that culminate between 140 and 200 ms (Bentin, Allison, Puce, Perez, & McCarthy, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996; Halgren, Raij, Marinkovic, Jousmaki, & Hari, 2000; Itier, Herdman, George, Cheyne, & Taylor, 2006; Liu, Higuchi, Marantz, & Kanwisher, 2000; Sams, Hietanen, Hari, Ilmoniemi, & Lounasmaa, 1999; for a review see Rossion & Jacques, 2008). The N170 and M170 have been shown to be highly sensitive to the perception of eyes and to be modulated by seen gaze direction, but with diverse results according to stimuli, designs, and tasks (Conty, N'Diaye, Tijus, & George, 2007; Itier et al., 2007; Latinus et al., 2015; Ponkanen, Alhoniemi, Leppanen, & Hietanen, 2011; Puce, Smith, & Allison, 2000; Rossi, Parada, Latinus, & Puce, 2015; Taylor, George, & Ducorps, 2001; Watanabe, Kakigi, Miki, & Puce, 2006; Watanabe, Miki, & Kakigi, 2002). Only a few studies varied head orientation together with gaze direction when examining modulation of these components by gaze direction. With EEG, Itier et al. (2007) found that the modulation of N170 to gaze direction was dependent on head orientation, with greater N170 to averted than direct gaze under frontal head view only. They suggested that gaze direction and head orientation

interact at a decision making level, rather than at an early perceptual processing stage. In contrast, when examining responses to apparent eye movement, Conty et al. (2007) found greater N170 to direct gaze independent of head orientation. In their study, only the N170 in response to averted gaze depended on head orientation, with greater N170 to averted gaze under frontal than deviated views of the face. This suggests that direct gaze may be processed at least to some extent independently of head orientation and that gaze direction and head orientation may be integrated early on, in the time window of the N170 and M170, at least when direct gaze is perceived. To our knowledge, no study has examined the sensitivity of M170 (in MEG) to gaze direction in combination with head orientation. For instance, Taylor, George, and Ducorps (2001) showed enhanced M170 for direct relative to averted gaze with eyes-only stimuli. Watanabe, Kakigi, Miki & Puce (2006) used full faces, but in frontal head views only. They showed enhanced M170 to gaze shifts from averted position toward the perceiver as compared to gaze shifts in the opposite direction—from straight to averted gaze direction. In contrast, Sato, Kochiyama, Uono, & Yoshikawa (2008) found greater M170 to averted than straight gaze in frontal face view. The superior temporal sulcus (STS) was involved in this effect.

We aimed to further characterize the dynamics of the early perceptual processing of gaze direction of neutral faces, as well as its interaction with head orientation. We combined EEG and MEG recordings, because although they are closely related high-temporal resolution brain imaging methods, EEG and MEG studies have led to different findings regarding the neural coding of gaze direction, as mentioned above. This may be due to the fact that they are optimally sensitive to different configurations of brain sources. Whereas EEG is sensitive to both radial and tangential components of brain sources, MEG is sensitive only to the tangential

component of brain sources (Ahlfors, Han, Belliveau, & Hamalainen, 2010).

Furthermore, magnetic fields decay faster over distance than electric currents do. As a consequence, EEG is relatively more sensitive than MEG to signals generated in different brain regions (Irimia, Van Horn, & Halgren, 2012). At the same time, electric currents, measured by EEG, are distorted and markedly diffused by the brain, skull, and skin tissues, while magnetic fields, measured by MEG, propagate without distortion through these tissues. These different properties are taken into account in source localization algorithms. It has therefore been argued that EEG is less powerful than MEG for localizing the cortical sources of event-related potentials / magnetic fields. A more refined view is that EEG and MEG can bring complementary information on the dynamics of information processing by the human brain, as shown by several EEG-MEG studies (Henson, Mouchlianitis, & Friston, 2009; Morel, Ponz, Mercier, Vuilleumier, & George, 2009; Watanabe, Kakigi, & Puce, 2003; see also Steinberg, Brockelmann, Rehbein, Dobel, & Junghofer, 2013). Their distinctive properties make their combination a powerful and informative tool for measuring brain activity with respect to neural generators (Irimia et al., 2012; Malmivuo, 2012).

We recorded electric and magnetic responses to frontal and deviated head views of neutral faces with direct and averted gaze in a gender categorization task. We focused on the early perceptual responses to the faces. Our hypothesis was that we would observe early coding of head direction at P1 (and probably M1) level (Itier et al., 2007); this would fit with the idea that head orientation is processed early on, as a coarse cue (Emery, 2000). Most importantly, we expected a modulation of both the N170 (in EEG) and M170 (in MEG) by gaze direction, but with possible differences with regard to the interaction between gaze direction and head orientation. We further used source localization to examine the involvement of the

different parts of the lateral occipito-temporal cortex in the effects obtained in EEG and MEG. This allowed us to highlight the involvement of different parts of the right superior temporal sulcus (STS) region, in line with the roles in gaze coding that have been proposed for the posterior and anterior parts of this region (Carlin & Calder, 2013).

2. MATERIALS AND METHODS

2.1 Participants

Fourteen healthy paid volunteers (4 women; mean age= 27.6 ± 1.7 yrs) provided written informed consent to participate in this study, which was approved by the French Comité Opérationnel pour l'Ethique dans les Sciences de la Vie of the Centre National pour la Recherche Scientifique. All were right-handed, had a right predominant eye, normal or corrected-to-normal vision and reported no previous history of neurological or psychiatric illness. One female participant was excluded from the analyses because she presented very prominent alpha rhythm.

2.2 Stimuli

We used the same stimulus set as George et al. (2001). These stimuli were 34 different unknown face photographs (17 male, 17 female faces, all with a neutral expression) taken under four different conditions of head orientation and gaze

direction: frontal and deviated head view with direct or averted gaze (Figure 1).

These face photographs were systematically taken under the same lighting and position conditions, with the eyes straight toward the camera / observer, or averted by 30°, and the head facing the camera (frontal head view) or rotated by 30° from the camera / observer (deviated head view). Each face was carefully centered in the image frame so that the edge of the nose between the two eyes always fell in the same location for frontal faces and for deviated faces. Rightwards and leftwards deviations of head orientation and/or gaze direction were obtained, by vertically mirroring the photographs that were initially taken using a rightward angle of deviation only (see George et al., 2001 for details). The stimuli were presented in greyscale on a black background. They were reduced in size so as to subtend on-screen a visual angle of about 5 degrees horizontally and 7 degrees vertically.

2.3 Procedure

The experiment took place at the MEG Centre of the Pitié-Salpêtrière Hospital in Paris. To minimize irrelevant time-effects and time-by-condition interactions within the EEG-MEG data, participants were allowed to look through print-outs of the 34 faces, under frontal and right and left deviated head views with congruent gaze direction, at their own pace, prior to recording. On average, the participants went through all the photos once, in about a minute. During the recording session, participants sat on a comfortable chair in a dimly lit electromagnetically shielded room. The stimuli were back-projected onto a screen inside the shielded room (viewing distance: 1.2 m) through a system including a video-projector placed outside of the room and two mirrors inside the room.

The experimental session consisted of four stimulus blocks comprising 136 face stimuli each. In each block, the 34 faces were shown, in a random order, one time in each of the following conditions: under frontal and deviated head views with direct and averted gaze directions. Rightwards and leftwards directions of deviation in gaze and/or head angle were presented in different blocks (two blocks per direction of deviation). Block order was counterbalanced across participants. Within each block, the stimuli were presented for 200 ms each, with a random interstimulus interval comprised between 1500 ms and 2500 ms. Stimuli were programmed to allow presentation timing to the millisecond, with triggers being sent to the MEG data acquisition system through parallel port, as well as the recording of participant's responses. The participants were instructed to fixate the screen centrally and to report the gender of the seen face as quickly and as accurately as possible, with a two-alternative button-press response. Male and female responses were given with left and right hand respectively, counterbalanced across participants.

2.4 Data collection

Magnetic fields were recorded on a whole-head MEG system with 151 axial gradiometers (Omega 151, CTF Systems, Port Coquitlam, B.C., Canada). This system includes seventeen external reference gradiometers and magnetometers that are used to apply a synthetic third-gradient to all MEG signals for ambient field correction. Three small coils were attached to reference landmarks on the participant (left and right preauricular points, plus nasion) in order to check head position at the beginning of each block. For all participants but one, electrical activity was recorded simultaneously with an amagnetic 64 Ag/AgCl unipolar electrode cap and processed by the MEG system. Electrode placement followed the extended International 10–20

system, including a row of low temporo-occipital electrodes (TP9-TP10, P9-P10, O9-O10, Iz). One male participant's head was too big to fit in the MEG system with the electrode cap on, so EEG was recorded using only 5 pasted electrodes placed at Cz, TP9, P9, TP10 and P10. Therefore this participant was included only in the ERP and ERF peak analyses, but not in the follow-up GFP analysis and source localization (see below). The reference electrode for EEG recording was placed on the bridge of the nose. Stimulus delivery, the triggering of EEG/MEG trial-by-trial acquisition and the recording of participants' behavioural responses were controlled by a computer (PC) running in MS-DOS mode with < 1 ms precision. The recording included the signal of a photodiode that detected the actual appearance of the face stimuli on the screen within the MEG room. This made it possible to correct for any delay introduced by the video projector and averaging ERPs and ERFs precisely time-locked to the actual onset of the face stimuli for each subject. On each trial, EEG/MEG signals were recorded for 1450ms, including a 200-ms pre-stimulus baseline. The sampling rate was 625Hz, 500pt/sweep, with a band pass of 0-100Hz for MEG and of 0.16 to 100Hz for EEG. Participants were asked to avoid blinking in the interval from stimulus onset to their response. Eye movements and blinks were recorded by two pairs of disposable electrodes placed above and below the right eye for vertical electrooculogram (EOG) and at the outer canthus of each eye for horizontal EOG. One extra-channel served as a control track, recording the signal derived from the stimulation system. Trials were reviewed off-line to reject any trial with eye movements, eye blinks, muscular activity, or any other type of movement-related artefact. Trials with incorrect responses to the gender task or with answers falling outside the range between 250ms and 1500ms after stimulus onset were also discarded. Event-Related Potentials (ERPs) and Magnetic Fields (ERFs) were then

computed between –200 ms and +350 ms, with baseline correction over the 200 ms pre-stimulus period, separately for Direct and Averted gaze conditions under Frontal and Deviated head views (mean number of trials averaged \pm SEM= 72.9 \pm 6.0 per condition). These data were filtered with a low-pass filter set at 30Hz. The overall means of the ERF and of the ERP across participants (for the 12 participants with complete electrode coverage) were also calculated.

2.5 Data analysis

2.5.1 Behavioral data.

Only correct answers falling between 250ms and 1500ms after stimulus onset were taken into account. The rate of correct answers and the mean RT of correct answers computed for each participant and for each experimental condition were submitted to an ANOVA with gaze direction and head orientation as within-subjects factors. We pooled over right and left sides of head and/or gaze deviation after having checked that this factor did not influence the results.

2.5.2 ERP/ERF analysis.

We first performed classical measurements of the parameters of early electromagnetic components. We measured the peak amplitude and latency of the P100 (EEG), the M100 (MEG), the N170 (EEG), and the M170 (MEG), using customized Matlab (The MathWorks, Inc.) scripts. The peak amplitude and latency of the P1 visual evoked potential were measured between 80 and 140 ms on the electrode where the P1 was maximum in the left and right posterior parieto-occipital

regions (P9/10, P7/8, P5/6, PO7/8, PO3/4, TP9/10, O9/10, and O1/2, except for the male participant with 5 EEG electrodes only where the P100 could be measured solely on P9/10 and TP9/10), for each participant and experimental condition. Similarly, the peak amplitude and latency of the M100 magnetic component were measured in the same time range on the magnetic sensor where the M100 was maximum in left and right posterior occipito-temporal regions, for each participant and condition (MLO11, MLO12, MLO21, MLO22, MLO31, MLO32, MLO33, MLP31, MLP32, MLT26, MLT34, MZPO2 in the left hemisphere and MRO11, MRO12, MRO21, MRO22, MRO32, MRO33, MRO42, MRO43, MRP21, MRP31, MRT22, MRT26, MRT33, MRT34, MRT41 in the right hemisphere).

The peak amplitude and latency of the N170 component were measured between 130 and 195 ms on the electrode where the N170 was maximum among the low temporo-occipital electrodes in both hemispheres (TP9/10, P9/10, PO9/10, O9/10), for each participant and condition. The peak amplitude and latency of the M170 magnetic component were measured in a similar time window on the occipito-temporal sensor where it culminated in each hemisphere, for each participant and condition (MLT13, MLT14, MLT15, MLT16, MLT24, MLT26, MLT33, MLT34, MLT35, MLT43, MLO22, MLO33, MLO43 in the left hemisphere, and MRT14, MRT23, MRT24, MRT33, MRT34, MRT42, MRT43, MRT44, MRP34, MRO22, MRO33, MRO43 in the right hemisphere).

These amplitude and latency measures were analyzed using ANOVAs with GAZE DIRECTION, HEAD ORIENTATION, and HEMISPHERE as within-subjects factors. For amplitude measures, the values on the right hemisphere (which were negative because they corresponded to magnetic fields directed inward) were multiplied by -1 prior to statistical analysis. Follow-up planned comparisons were performed using

two-tailed Student t-test when significant interactions were found. We report effect sizes of statistically significant effects in the form of partial eta-squared (η^2) or Cohen's d.

2.5.3 GFP analysis

We then used global field power (GFP) (Lehmann & Skrandies, 1980) to achieve a global measurement of the EEG and MEG evoked activities respectively. The GFP of the ERP and the ERF obtained under each condition of gaze direction and head orientation was computed for the 12 participants who had both MEG and complete electrode coverage for EEG. GFP was calculated for each time point of the filtered and averaged epochs using Equation 1 for ERP and Equation 2 for ERF.

$$GFP = \sqrt{\frac{\sum_{i=1}^N (u_i - \bar{u})^2}{N}}, \quad \text{Equation 1}$$

$$GFP = \sqrt{\frac{\sum_{i=1}^N (u_i)^2}{N}} \quad \text{Equation 2}$$

with N, the number of electrodes (or magnetic sensors), u_i , the event-related electric potential (or magnetic field) on electrode (or magnetic sensor) i, and \bar{u} the mean value of u_i across electrodes (or magnetic sensors) at the considered time point.

We used repeated-measures time point-by-time point ANOVA with GAZE DIRECTION and HEAD ORIENTATION as within-subjects factors to analyse these GFP data. The analysis was performed using the STEN toolbox developed by Jean-François Knebel (<http://www.unil.ch/fenl/home/menuinst/infrastructure/software-analysis-tools.html>). In order to compensate for multiple comparisons across time points, we used a temporal stability criterion with a threshold of $p < .05$ for a minimal

duration of at least 10 ms to assess the time intervals of statistically significant effects or interaction. Follow-up planned comparisons using two-tailed Student t-test were performed when significant interactions were found. In addition, non-parametric Wilcoxon signed-rank tests were performed to confirm the significant effects found with parametric statistical tests.

2.5.4 Source localization

Source localization was performed with Brainstorm software (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011), which is documented and freely available for download online under the GNU general public license (<http://neuroimage.usc.edu/brainstorm>). Cortical current source density mapping was obtained using a distributed source model consisting in ~15,000 current dipoles in each participant and condition. Dipole locations were constrained to the cortical mantle of a generic brain model built from the standard brain of the Montreal Neurological Institute using the BrainSuite software package (<http://neuroimage.usc.edu>). Dipole orientations were unconstrained. We then used the following forward models: Overlapping spheres for MEG (Huang, Mosher, & Leahy, 1999) and three-shell sphere (taking into account the different electrical conductivities of brain tissues—i.e. skin, skull, cerebrospinal fluid) for EEG (Huang et al., 1999), using the cortical surface as the potential source of the electric and magnetic signals. The noise covariance matrix was computed using the baseline periods of the ERP / ERF obtained under every condition. Finally, we computed the inverse model using the weighted minimum-norm estimate

approach (wMNE), and estimated the amplitude for each of the 15000 current dipoles distributed across the cortical surface, for ERP and ERF separately.

We first computed the overall mean of source activity in the time windows of the N170 and M170. This was done by averaging current dipole moments over a 20 ms time window centred on the overall mean peak latency of the N170 and M170 respectively, across participants. We next extracted the source activity across the entire cortical surface in the time windows identified by the GFP analysis. Mean source activity in the time windows of interest was extracted in NIfTI format from Brainstorm software, for each condition and each participant. These source data were entered into a flexible factorial general linear model (GLM) design with GAZE DIRECTION and HEAD ORIENTATION as within-subjects factors and SUBJECT as between-subjects factor, using Statistical Parametric Mapping (SPM8) software (Wellcome Department of Cognitive Neurology, London, UK), implemented on Matlab 2011b (Math Works Inc., Natick, MA, USA). We computed a second-level random effect analysis. The GLM estimates the error variance for each condition of interest across participants (Holmes & Friston, 1998) and therefore provides a generalization to the population from which data are acquired. In our flexible GLM, we incorporated the SUBJECT as between-subjects factor to balance the difference among participants (Gläscher & Gitelman, 2008). We used a statistical threshold of $p < .005$, with a minimum cluster size of 20 voxels to assess the regions involved in the effects identified. These regions were labelled using the Anatomy toolbox (Eickhoff et al., 2007; Eickhoff et al., 2005).

3. RESULTS

3.1 Behavioural results

The overall rate of correct answers to the gender identification task was 95.1% (range across conditions: 85.3- 100%) and the overall mean reaction time (RT) was 581 ± 13 ms (mean \pm SEM). The 2 x 2 ANOVA with GAZE DIRECTION and HEAD ORIENTATION as within-subjects factors did not reveal any effect of either gaze direction or head orientation, either on correct answer rate or on RT ($F < 1$).

3.2. Early ERP and ERF peak analysis: P/M100 and N/M170

P100: The P100 amplitude, depicted in figure 2, was significantly greater for deviated ($8.1 \pm 0.9 \mu\text{V}$; 95% confidence interval, CI = [6.1; 10.0 μV]) than for frontal ($7.0 \pm 1.0 \mu\text{V}$; CI = [5.0; 9.1 μV]) HEAD ORIENTATION ($F(1,12)=7.1$, $p=.02$; $\eta^2 = 0.37$). We found no other significant effect nor any interaction on the P100 amplitude. In particular, the P100 amplitude did not reveal any significant effect of GAZE DIRECTION. The overall mean P100 peak latency was 108 ± 3 ms. There was no significant effect of GAZE DIRECTION, HEAD ORIENTATION, or HEMISPHERE on P100 peak latency except for a statistically significant three-way interaction between these factors ($F(1,12)=4.8$, $p < .05$, $\eta^2 = 0.29$), which reflected that incongruent head orientation and gaze directions yielded slightly later P100 (mean = 108 ± 3 ms; CI=[98; 112 ms]) than congruent ones (mean = 105 ± 3 ms; CI=[101; 114 ms]) in the left hemisphere only ($t(12)=2.3$, $p < .05$; $\eta^2 = 0.30$).

M100: The M100 was identified in 11 out of the 13 participants (one participant showed a bipolar component of reverse polarity in the latency range of the M100 and another one had an identifiable right M100 but no identifiable left M100). Its latency

and amplitude parameters did not show any significant effect of GAZE DIRECTION, HEAD ORIENTATION, or HEMISPHERE, and there was no interaction among these factors either (all $F(1,10) < 4.5$, all $p > .05$).

N170: The peak amplitude of the N170 showed a trend to an effect of GAZE DIRECTION ($F(1,12)=3.3$, $p = .09$; $\eta^2=0.22$), which was further qualified by a significant interaction with hemisphere ($F(1,12)=7.4$, $p < .02$; $\eta^2=0.38$). This reflected a small but reliable effect of GAZE DIRECTION that reached significance over the right hemisphere only ($t(12)=2.7$, $p < .02$; $\eta^2=0.38$), with enhanced right N170 to faces with direct (relative to averted) gaze (*Table 1* and *Figure 3*). Closer examination of individual subject's data revealed that the N170 was greater for direct relative to averted gaze under frontal or deviated head or both in all participants but one, accounting for the small but reliable net effect of gaze, in the right hemisphere.

M170: The peak amplitude of the M170 showed a significant interaction between HEAD ORIENTATION and GAZE DIRECTION ($F(1,12)=8.6$, $p = .01$; $\eta^2=0.42$). This reflected an effect of GAZE DIRECTION – with greater M170 to direct than averted gaze, which reached significance under deviated head views only ($t(12)=2.9$, $p = .01$; $\eta^2=0.41$) (*Table 2* and *Figure 4*). The effect of GAZE DIRECTION was not significant when the faces were seen under frontal head view ($p > .10$). There was no other main effect nor interaction on either M170 amplitude or latency.

3.3 Global Field Power (GFP) analysis

We analyzed the GFP of ERP and ERF across time in order to confirm the effects identified on the peak amplitude and latencies of early ERP and ERF components.

EEG: The time-wise ANOVA performed on the GFP of ERP revealed first a main effect of HEAD ORIENTATION between 93 and 116 ms. The averaging of the GFP in this time window showed a significantly larger GFP for the deviated head orientations ($2.08 \pm 0.26 \mu\text{V}$) than for the frontal head orientations ($1.78 \pm 0.24 \mu\text{V}$) ($F(1,11) = 30.81$, $p < .001$, $\eta^2 = 0.75$; (Figure 5.A, upper row). A non-parametric Wilcoxon signed-rank test confirmed this result, $Z = 2.98$, $p < .003$. This corresponded to the effect of head orientation identified on the P100 amplitude. Second, the time-wise ANOVA on the GFP of ERP revealed a main effect of GAZE DIRECTION between 171 and 186 ms (Figure 5.A, second row). The GFP average in this time window showed a larger GFP for the direct gaze conditions ($2.36 \pm 0.23 \mu\text{V}$) than for the averted gaze conditions ($2.15 \pm 0.22 \mu\text{V}$), independently of head orientation ($F(1,11) = 10.62$, $p < .005$, $\eta^2 = 0.33$). The Wilcoxon signed-rank test confirmed this result, $Z = 2.2$, $p < .023$. This confirmed the effect of gaze direction identified on the N170 peak amplitude. There was no significant interaction between GAZE DIRECTION and HEAD ORIENTATION identified in the GFP analysis of ERP.

MEG: The time-wise ANOVA on the GFP of ERF revealed an interaction between GAZE DIRECTION and HEAD ORIENTATION between 134 and 162 ms, that is, in the time window of the M170. The GFP average in this time window confirmed this significant interaction ($F(1,11) = 8.3$, $p < .014$, $\eta^2 = 0.41$) and showed that it reflected a larger GFP for the direct gaze condition ($89.12 \pm 9.39 \text{ fT}$) than the averted gaze condition ($80.15 \pm 9.32 \text{ fT}$) when the head was deviated ($t(11) = 2.2$, $p = .04$, Cohen's $d = 0.71$; Figure 5.B, lower row). The effect of gaze direction was not significant when the head view was frontal. A Wilcoxon signed-rank test confirmed this result, $Z = 2.19$, $p < .028$. Additionally, the interaction reflected a larger GFP for the frontal head

view (88.81 ± 9.56 fT) than the deviated head view (80.01 ± 9.25 fT) in the averted gaze condition ($t(11) = 3.3$, $p = .006$, Cohen's $d = 1.28$; no significant effect of head orientation in the direct gaze condition). A Wilcoxon signed-rank test confirmed this result, $Z = 2.66$, $p < .008$. There was no other significant effect on the GFP of ERF.

3.4 Source localization

For illustrative purposes, we first localized the sources of the N170 and M170. To this aim, the current dipole moments obtained were averaged across conditions and participants in a 20 ms time window centred on the overall mean peak of the N170 (152 ms) and M170 respectively (151 ms).

The N170 sources involved a widespread network, including the bilateral STS extending into the parietal region, the fusiform gyrus and the middle and inferior occipito-temporal cortex regions (Figure 6.A). The M170 sources involved a somewhat more restricted network, involving mainly the inferior occipital and the lateral fusiform gyrus (Figure 6.B).

We then extracted the source activity during the periods where the GFP analysis indicated significant effects of gaze direction, head orientation, and/or interaction between these factors in EEG and MEG respectively.

Sources of the HEAD ORIENTATION effect in EEG

Source analysis of the HEAD ORIENTATION effect (deviated > frontal head views) between 93 and 116 ms indicated the involvement of the left extrastriate occipital cortex in its medial portion, extending into precuneus (figure 7). The MNI coordinates of the maximally activated voxel was [MNI x y z: 20 -92 1]. It should however be kept in mind that these coordinates are bound to be approximate due to the limited spatial

resolution of the source localization performed and they are reported only for indicative purpose.

Sources of the GAZE DIRECTION effect in EEG

The contrast of Direct versus Averted Gaze on the mean amplitude of the sources of the ERP between 171 and 186 ms pointed to the involvement of the anterior part of the right temporal cortex, including the anterior STS (MNI coordinates of the maximally activated voxel: [62 0 4] (figure 8).

Sources of the interaction between GAZE DIRECTION and HEAD ORIENTATION in MEG

We then performed flexible GLM analysis of the mean amplitude of the sources of the ERF between 134 and 162 ms, to identify candidate regions for the interaction between GAZE DIRECTION and HEAD ORIENTATION, which was observed in this time window on the GFP of ERF (figure 9.A). This demonstrated the involvement of a set of regions lateralized to the right hemisphere, comprising the right inferior occipital cortex region [MNI coordinates: 46 -73 -3] extending to the fusiform gyrus [44 -59 -13], and the right posterior STS region [64 -42 10]. We further tested the simple main effect of gaze direction (direct gaze > averted gaze) in deviated head view (figure 9.B). This confirmed the involvement of the right inferior occipito-temporal cortex region [MNI coordinates: 37 -75 -1] and the right pSTS region [MNI coordinates: 67 -41 11].

4. Discussion

This study aimed to investigate the dynamics of the early perceptual processing of gaze direction and its interaction with head orientation by using combined EEG and MEG recording. Our main result was the differentiated effect of gaze direction on the N170 in EEG and M170 in MEG, with greater response to direct gaze under deviated head view on M170 peak amplitude and between 134 and 162 ms in GFP analysis, followed by a main effect of gaze (direct gaze > averted gaze) on N170 peak amplitude and between 171 and 186 ms in GFP analysis. These effects involved different parts of the right lateral temporal cortex, peaking in the posterior and anterior STS regions respectively, shedding new light on the timecourse of gaze direction processing in this region.

We found differentiated effects of gaze direction on the N170 (in EEG) and M170 (in MEG), corroborated by GFP analysis of ERP and ERF. While converging with prior studies that showed effects of gaze direction in the N170/M170 time range (e.g., Conty et al., 2007; Itier et al., 2007; Latinus et al., 2015; Puce et al., 2000; Watanabe et al., 2006; Yokoyama, Noguchi, & Kita, 2013), our findings reveal several important properties of gaze direction processing. First, they emphasize the early integrated coding of gaze and head cues to the direction of others' attention (for reviews, see Langton, 2000; Nummenmaa & Calder, 2009). The interaction between gaze direction and head orientation found on the M170 and between 134 and 162 ms in the GFP analysis underscores the sensitivity of the human brain to direct gaze when it is seen in a deviated head view. Preference for direct gaze in deviated head orientation has previously been highlighted in different tasks, such as visual search tasks and memory tasks (Conty et al., 2007; Conty et al., 2006; Senju & Hasegawa,

2005; Vuilleumier et al., 2005). It has been proposed that the incongruence between gaze direction and head orientation emphasizes the directional intent of the gaze and therefore the saliency of direct gaze under deviated head view (Conty et al., 2006). It is also possible that the brain is particularly sensitive to incongruent stimuli because these convey conflicting information and need additional processing resources to be coded and deciphered. Consistent with this idea, it has been shown that we detect congruent gaze direction and head orientation cues faster than incongruent ones (Itier et al., 2007; Langton, 2000; Pageler et al., 2003; Seyama & Nagayama, 2002; Todorovic, 2009).

The sources of the gaze by head interaction effect and of the simple main effect of direct versus averted gaze in deviated head view involved the face perception complex (inferior occipital cortex, fusiform gyrus, and pSTS regions) in the right hemisphere. These regions form the core face processing system of the human brain; they have been proposed to be involved in the processing of invariant and variant aspects of faces (Haxby et al., 2000; Hoffman & Haxby, 2000; Ishai, 2008). The inferior occipital and fusiform gyrus regions play an essential role in the encoding of faces and facial features (Goffaux, Gauthier, & Rossion, 2003; Liu, Harris, & Kanwisher, 2010; Schiltz & Rossion, 2006). They may be particularly activated by incongruent gaze direction and head orientation (Itier et al., 2007; Langton, 2000; Seyama & Nagayama, 2002; Todorovic, 2009), because – as mentioned above – this combination of features conveys conflicting information. Moreover, functional brain imaging and clinical neuropsychological studies point to the STS as a key brain region in the processing of variant aspects of faces (Bernstein & Yovel, 2015; Haxby, Hoffman, & Gobbini, 2000; Hoffman & Haxby, 2000; Ishai, 2008). In particular, it seems to play an essential role in social attention (i.e., in the processing of biological

cues to the direction of others' attention) (e.g. Akiyama et al., 2006; Sato et al., 2008), particularly in the right hemisphere (for a review see Allison, Puce, & McCarthy, 2000; George & Conty, 2008). The posterior part of the right STS (pSTS) has been shown to be activated in response to averted relative to direct gaze presented in frontal head views (Hoffman & Haxby, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998) and in response to direct gaze relative to averted gaze in deviated head views (Pelphrey, Viola, & McCarthy, 2004). It has been proposed to be involved in the coding of gaze direction in interaction with head orientation (Carlin & Calder, 2013) and to be sensitive to the intentionality of gaze (Calder et al., 2007; Pelphrey, Singerman, Allison, & McCarthy, 2003; Pelphrey et al., 2004; Pierno et al., 2006). A recent model proposed that STS is a key region for the integration of dynamic cues from faces and bodies, which are essential as signatures of individual identity as well as for social cognition (Bernstein and Yovel, 2015). Our results are in line with these proposals (for a review, see Nummenmaa & Calder, 2009). Although we used static faces, gaze direction and head orientation are dynamic cues in nature. These static, neutral faces varying in gaze direction and head orientation activated the STS region and functionally related inferior occipital and fusiform gyrus regions of the core face processing system (Bernstein and Yovel, 2015; Haxby et al., 2000; Ishai, 2008). The results also emphasized the importance of direct gaze (here in deviated head view, but see also below), and they further show the early activation of the STS region during the processing of faces with different head and gaze orientations.

The pSTS region was not the only part of the STS involved in our study. There was a main effect of gaze direction on the N170, with greater N170 in response to faces with direct than averted gaze on right occipito-temporal electrodes, and source

analysis of the main effect of gaze between 171 and 186 ms (as identified by the GFP analysis of ERP data) pointed to the involvement of the anterior lateral temporal cortex region centered on the anterior STS (aSTS), in the right hemisphere. Like the right pSTS, the right aSTS has been shown to be activated in response to gaze direction (Calder et al., 2007; Kingstone, Tipper, Ristic, & Ngan, 2004). However, in contrast to pSTS, it has been proposed to underpin a head view-independent representation of gaze direction (Carlin & Calder, 2013; Carlin, Calder, Kriegeskorte, Nili, & Rowe, 2011; De Souza, Eifuku, Tamura, Nishijo, & Ono, 2005; Perrett et al., 1985). This is in direct agreement with the present results, which further provide information on the timeline of activations within the STS region. It appears that the right pSTS region – in association with the right inferior occipital and fusiform gyrus regions – was activated earlier than the right aSTS region. This accords with the well-known posterior-to-anterior gradient of information processing along the visual pathway (Courtney, Ungerleider, Keil, & Haxby, 1997; Damasio, Tranel, & Damasio, 1990; Felleman & Van Essen, 1991; Haxby et al., 1994; Ungerleider, 1995). It suggests that the anterior regions of the STS may use the output of its posterior regions to code information relative to gaze direction, particularly eye contact, independently of head view (Perrett et al., 1992; see also Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005; Wicker, Perrett, Baron-Cohen, & Decety, 2003). In other terms, there seems to be an initial stage of gaze processing in the right pSTS region, encompassing the analysis of head view, with greater responses to direct gaze in deviated head view—which may constitute a particularly salient stimulus (Conty et al., 2007; Conty et al., 2006; Senju & Hasegawa, 2005; Vuilleumier et al., 2005). This is followed by view-invariant coding of gaze direction in the aSTS region, with greater response to direct than averted gaze, which may reflect

the essential role of gaze contact in social interactions (George & Conty, 2008; Kleinke, 1986; Patterson, 2011). These processing stages take place in close sequence during the perceptual analysis of faces, within the time range of the N170 / M170 in response to those faces.

Additionally, a main effect of head orientation was found on P1 peak amplitude and between 93 and 116 ms on the GFP of ERP data. It was associated with activity in the medial occipital extrastriate region, lateralized to the left hemisphere. This early differential effect corroborates a previous study (Itier et al., 2007) that also showed larger P1 for faces with deviated than frontal head orientation. Given the occipital sources associated with this effect, it is likely that it was mainly related to low-level visual differences between frontal and deviated head views of faces. This suggests that head orientation may be first coded at an early stage of visual processing, as reflected by the P1 component, mainly based on broad low-level analysis of the facial features (Itier et al., 2007). Then, as the perceptual analysis of faces unfolds, as assessed by the N170 and M170, information from both gaze direction and head orientation is extracted, with initial greater responses to direct gaze in deviated head view, followed by overall greater responses to direct than averted gaze.

It may be noted that we used a gender categorization task, that is, a task that did not require explicit processing of gaze direction and where gender was a variable orthogonal to the head orientation and the gaze direction variables. Numerous studies have demonstrated mutual influences or automatic processing of gaze direction and/or head orientation in tasks where one of these variables was either explicitly processed (such as gaze direction discrimination tasks or head orientation discrimination tasks) or implicitly processed, but still relevant to the task (such as directional decision tasks or spatial tasks not related to the head or gaze direction)

(Conty et al., 2007; Itier et al., 2007; Langton, 2000; Langton & Bruce, 2000; Latinus et al., 2015; Pageler et al., 2003; Seyama & Nagayama, 2002). This has raised questions regarding the automatic nature of the processing of cues to the direction of others' attention, particularly eye gaze direction (Cooper, Law, & Langton, 2013; Framorando, George, Kerzel, & Burra, 2017; Langton & Bruce, 2000), because the eye region is considered to be the most salient region of faces (Yarbus, 1967). Some authors proposed that gaze direction and head orientation are automatically processed, regardless of task demand, but that they may be integrated at late—decision making—stages (Itier et al., 2007; see also Langton et al., 2000). In the present study, we show that gaze direction and head orientation are coded by the brain early on, and that they interact early on, at the stage of the perceptual analysis of faces as assessed by the M170 and N170, in an incidental gender categorization task. This is in line with studies that demonstrated unconscious processing of gaze (Stein et al., 2011 & Sterzer, 2011; Yokoyama et al., 2013). It emphasizes the saliency of the cues to the direction of others' attention, in particular the cues that may signal an intent to communicate, such as direct gaze under deviated head view. The early neural coding of such cues may be key to adaptive behavior (Emery, 2000).

There was no effect of gaze direction on the gender categorization task in the present study. This contrasts with the results of Macrae et al. (2002), who reported faster gender categorization for direct-gaze faces than for averted-gaze faces. This discrepancy may be explained by the high repetition rates of the faces in our study. Indeed, for the purpose of ERP and ERF computation in the present study, each face was presented 4 times (under each of the four experimental conditions of direct / averted gaze in frontal / deviated head view) in each block, and there were 4 blocks

of stimuli. In contrast, a unique presentation of faces was used in Macrae et al. (2002, Expe. 1) (with different individuals' faces used under each combination of gaze and headview). It is possible that this high repetition rate wiped out any effect of gaze direction on gender categorization, both by reducing the relevance of gaze direction for the face processing and by rendering the task monotonous and relatively automatic.

Some previous studies reported different effects of gaze direction on occipito-temporal brain responses to faces. For instance, in an fMRI study, Pageler et al. (2003) found an interaction between gaze direction and head orientation, but only in the fusiform gyrus and with larger activation for direct than averted gaze in frontally viewed faces, not in deviated views of faces. In a previous fMRI study using the same stimuli as the present study but in a blocked design, we found a main effect of gaze direction in the fusiform gyrus (George et al., 2001). Some ERP studies found effects of gaze direction on the N170 but with an effect opposite to ours, i.e. greater N170 to averted than direct gaze (Itier et al., 2007; Latinus et al., 2015; Puce et al., 2000). It is likely that these discrepancies may be accounted for by differences in the nature of the stimuli used (static gaze versus gaze movement; frontal and / or deviated head views of faces; numerous unique versus few highly repeated face exemplars) and in the task (implicit or incidental versus explicit gaze and face processing). Note also that later effects of gaze, in the time range of the P300 component, have previously been reported (Conty et al., 2007; Itier et al., 2007). These late activities were not analyzed in the present study, because we focused on the dynamics of the early perceptual coding of gaze direction and head orientation.

The present study emphasizes the complementarity of EEG and MEG for the investigation of the dynamics of brain activities. EEG and MEG are complementary

because of the different physical properties of electric currents and magnetic fields (Anogianakis et al., 1992; Garnero, Baillet, & Renault, 1998; Supek & Aine, 2014). Thus, as mentioned in the introduction, EEG is sensitive to both radial and tangential components of brain sources, while MEG is sensitive only to the tangential component of brain sources (Irimia et al., 2012). Another important aspect is that electric currents are distorted and markedly diffused by the brain, skull, and skin tissues, while magnetic fields propagate without distortion through these tissues, but with faster decay as a function of distance. As a consequence, at any point in time, EEG tends to integrate the activity from more brain sources than MEG does. These different properties may explain why the combination of EEG and MEG allowed us to reveal differentiated effects of gaze direction in the early (134-162 ms) and late (171-186 ms) time intervals of the M170 and N170 (respectively), involving different regions of the occipito-temporal cortex, along the STS.

It is worth mentioning a limitation of our study, related to the limited sample of subjects on which our results are based. Sample size has recently become a growing concern in neuroscience, because it causes problems with replicability (Button et al., 2013; Ioannidis, 2015; OpenScienceCollaboration, 2015). On one hand, it has been argued that low powered studies exhibit greater evidence, because they are less likely to report effects with small and trivial effect sizes (Friston, 2012). On the other, they result in uncertainty in the results (or enlarged confidence intervals) and in inflated effect sizes (Ingre, 2013). We provide effect sizes to allow full assessment of our results. Furthermore, for the key GFP analyses on which neural source localization investigation was based, we ran non-parametric Wilcoxon signed-rank tests in addition to classical analyses of variance. This non-parametric test is particularly appropriate for small samples. Therefore, we are confident in the

reliability of our results, even if it is important to keep in mind our sample size limitation. One may also note that our sample of subjects was mostly male. To our knowledge, no previous study examined gender differences in the sensitivity of N170 or M170 to gaze direction and head orientation. At the behavioural level, it has been suggested that female participants may be more sensitive to gaze direction than male participants, because they show greater attentional shift in responses to averted gaze cues (Bayliss, di Pellegrino, & Tipper, 2005; Cooney, Brady, & Ryan, 2017; Frischen et al., 2007). If anything, this would predict greater brain responses to gaze direction in female than male participants. In future studies it will be interesting to test if this may influence the early coding of gaze direction and head orientation as reported here.

5. Conclusion

This study examined how gaze direction processing unfolds over time and its interaction with head orientation. By using combined EEG and MEG recording, it revealed an integrated processing of gaze and head cues in the early time range of the M170 (134-162 ms) followed by direct versus averted gaze processing independent of head orientation (171-186 ms, in ERP data). Source localization suggested that this multiple stage processing relied on a posterior-to-anterior right occipitotemporal network, involving the posterior and anterior parts of the STS region. These findings emphasize the complementarity of MEG and EEG for studying dynamic brain responses to complex social stimuli such as those formed by faces.

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Fig 1. Example stimulus. An example stimulus is presented under the four experimental conditions of the study.

Fig 2. Effect of gaze direction on P1. The time course of the overall mean of the ERP across participants is shown for the four experimental conditions (direct / averted gaze in frontal / deviated views of faces) on 6 occipital electrodes (O1, Oz, O2, O9, Iz, O10). This allows visualizing the effect of head orientation on P1. On top left, the topography of P1 at its peak is shown (overall mean of the 12 participants with whole-head electrode coverage).

Fig 3. N170 for direct and averted gaze. The time course of the overall mean of the ERP across participants is shown on typical left (TP9, P7, P9, PO7) and right (TP10, P8, P10, PO8) occipito-temporal electrodes for the direct (in black) and averted (in red) gaze conditions (averaged across head orientations). There was a small but reliable effect of gaze direction on the right occipito-temporal electrodes (as pointed out by the red and black arrows), with greater N170 for direct than averted gaze. On top left, left and right side views of the head show the topography of N170 at its peak latency (overall mean of the 12 participants with whole-head electrode coverage).

Fig 4. M170 for direct and averted gaze seen in frontal and deviated head views.

The time course of the overall mean of the ERF across participants is shown on typical left (MLT25, MLT26) and right (MRT33, MRT42) temporal sensors for the four experimental conditions: direct (in black and blue) and averted (in red and green) gaze in frontal and deviated head views. The blue and green arrows highlight the significant interaction between GAZE DIRECTION and HEAD ORIENTATION observed on the M170 peak amplitude, which reflected a statistically greater M170 for direct (blue) than averted gaze (green) in deviated head view. The effect of gaze direction did not reach significance in frontal head view. On top left, left and right side views of the head show the topography of M170 at its peak latency (overall mean of the 13 participants).

Fig 5. GFP analysis. We analyzed the GFP of ERP (in A) and ERF (in B) across time. The time windows where the effects were statistically significant (with $p < .05$ for at least 10 ms) are colored in black. This analysis revealed:

A) a main effect of HEAD ORIENTATION between 93 and 116 ms (first row) and a main effect of GAZE DIRECTION between 171 and 186 ms (second row) on the GFP of ERP. The bar plots show the GFP values averaged over each of these two time

windows, highlighting the main effect of HEAD ORIENTATION in the first time window and of GAZE DIRECTION in the second time window.

B) an interaction between GAZE DIRECTION and HEAD ORIENTATION between 134 and 162 ms on the GFP of ERF. The bar plot shows the GFP values averaged in this time window for the four experimental condition, highlighting the effect of gaze direction (GFP for direct gaze > GFP for averted gaze) in deviated head view and the effect of head orientation (frontal > deviated) in the averted gaze condition.

Fig 6. Sources of the N170 and M170. Overall mean of the cortical current dipole moments in the time window of the N170 (for EEG, in A) and M170 (for MEG, in B). Only sources with an activity reaching at least 60% of the maximal activity in the examined time window are represented, in shades of red for the EEG and in shades of purple to red for the MEG. This revealed a more distributed set of activated sources for the N170 than the M170.

Fig 7. SPM maps of the HEAD ORIENTATION effect between 93 and 116 ms in EEG. We extracted the mean amplitude of the sources of ERP between 93 and 116 ms for the four experimental conditions of gaze direction and head orientation, and we modeled it with a flexible GLM in order to identify the candidate regions for the effect of HEAD ORIENTATION identified on the GFP of ERP in this time window. This revealed the involvement of left medial occipital regions, extending to the precuneus (with $p < .005$ and a cluster size ≥ 20 voxels).

Fig 8. SPM maps of the GAZE DIRECTION effect between 171-186 ms in EEG.

The contrast of Direct versus Averted Gaze revealed that the anterior part of the right temporal cortex centred on the anterior STS region was the candidate region for the main effect of GAZE DIRECTION observed between 171 and 186 ms on the GFP of ERP ($p < .005$, cluster size ≥ 20 voxels).

Fig 9. SPM maps of the interaction between GAZE DIRECTION and HEAD ORIENTATION (in A) and of the simple main effect of Direct versus Averted Gaze in Deviated head view (in B), between 134 and 162 ms, in MEG. A) The flexible GLM analysis of the interaction between GAZE DIRECTION and HEAD ORIENTATION performed on mean source amplitude of ERF between 134 and 162 ms revealed the involvement of the right inferior occipital cortex regions extending to the fusiform gyrus region and of the right pSTS region. B) The contrast of Direct versus Averted Gaze in Deviated Head view confirmed the involvement of these regions in the integration of gaze direction and head orientation. The statistical threshold for all SPM maps was $p < .005$ and cluster size ≥ 20 voxels.

Table 1 – Peak amplitude and latency of the N170 (overall mean across participants \pm SEM, and 95% CI in square brackets) under the four experimental conditions of gaze direction and head orientation, in the right hemisphere (Right) and left hemisphere (Left)

	Frontal head		Deviated head	
	Direct gaze	Averted gaze	Direct gaze	Averted gaze
Right	$-9.63 \pm 1.01 \mu V$ [-11.83; -7.43 μV]	$-8.63 \pm 1.15 \mu V$ [-11.14; -6.12 μV]	$-8.96 \pm 1.14 \mu V$ [-11.43; -6.48 μV]	$-8.56 \pm 0.90 \mu V$ [-10.52; -6.59 μV]
	155 ± 4 ms [146;164 ms]	156 ± 3 ms [148;163 ms]	158 ± 3 ms [152;165 ms]	157 ± 3 ms [150;163 ms]
Left	$-10.79 \pm 1.34 \mu V$ [-13.70; -7.87 μV]	$-10.85 \pm 1.23 \mu V$ [-13.52; -8.17 μV]	$-10.46 \pm 1.25 \mu V$ [-13.18; -7.74 μV]	$-9.92 \pm 1.26 \mu V$ [-12.67; -7.17 μV]
	154 ± 2 ms [149;159 ms]	155 ± 2 ms [150;160 ms]	157 ± 2 ms [152;163 ms]	155 ± 2 ms [151;159 ms]

Table 2 – Peak amplitude and latency of the M170 (overall mean across participants \pm SEM, and 95% CI in square brackets) under the four experimental conditions of gaze direction and head orientation, in the right hemisphere (Right) and left hemisphere (Left)

	Frontal head		Deviated head	
	Direct gaze	Averted gaze	Direct gaze	Averted gaze
Right	-233.3 \pm 27.8 fT [-172.9; -293.8 fT]	-255.9 \pm 32.0 fT [-186.2; -325.6 fT]	-252.4 \pm 29.6 fT [-187.8; -316.9 fT]	-235.1 \pm 29.0 fT [-171.9; -298.4 fT]
	151 \pm 3 ms [144; 159 ms]	151 \pm 4 ms [143; 158 ms]	151 \pm 4 ms [143; 159 ms]	151 \pm 4 ms [144; 159 ms]
Left	257.4 \pm 22.5 fT [208.4; 306.4 fT]	283.4 \pm 23.7 fT [231.8; 335.1 fT]	274.6 \pm 22.4 fT [225.7; 323.5 fT]	256.3 \pm 23.7 fT [204.7; 308.0 fT]
	149 \pm 3 ms [142; 156 ms]	149 \pm 4 ms [141; 157 ms]	151 \pm 3 ms [143; 159 ms]	149 \pm 3 ms [142; 156 ms]

Highlights:

- We investigated the spatio-temporal dynamics of gaze perception using combined EEG and MEG.
- The M170 was sensitive to gaze direction and head orientation.
- The N170 was sensitive to gaze direction regardless of head orientation.
- These modulations involved the pSTS and the aSTS respectively.

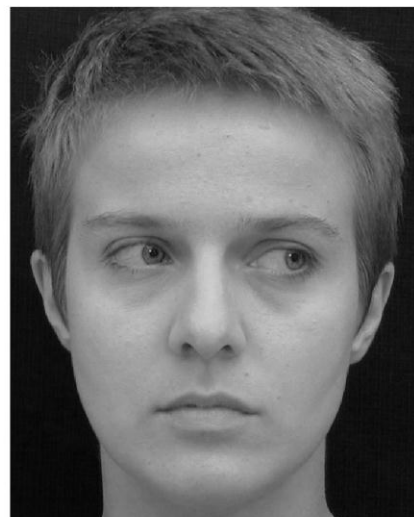
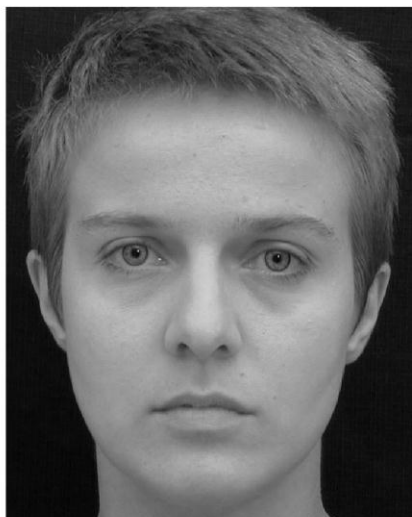
Gaze Direction

Direct

Averted

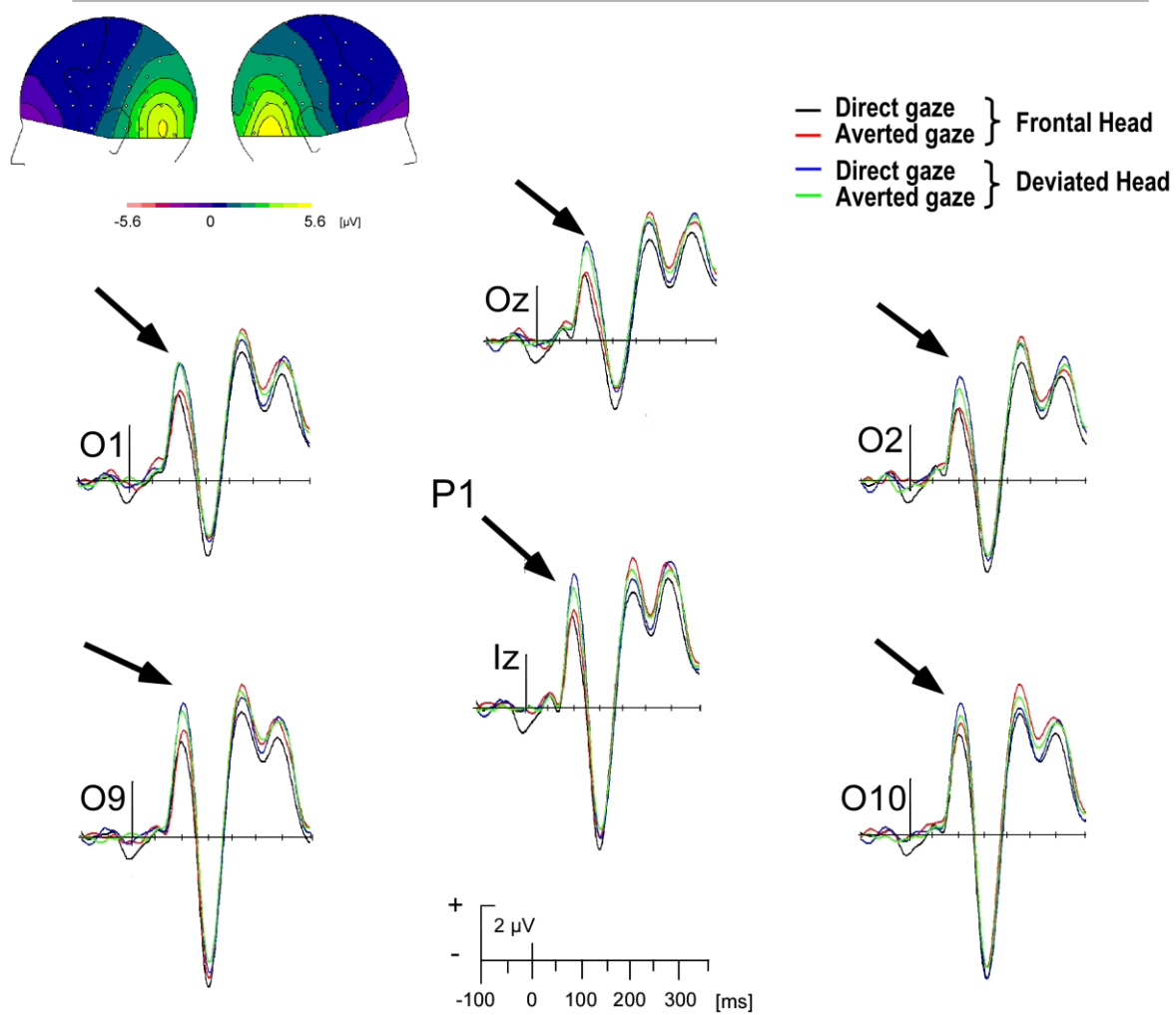
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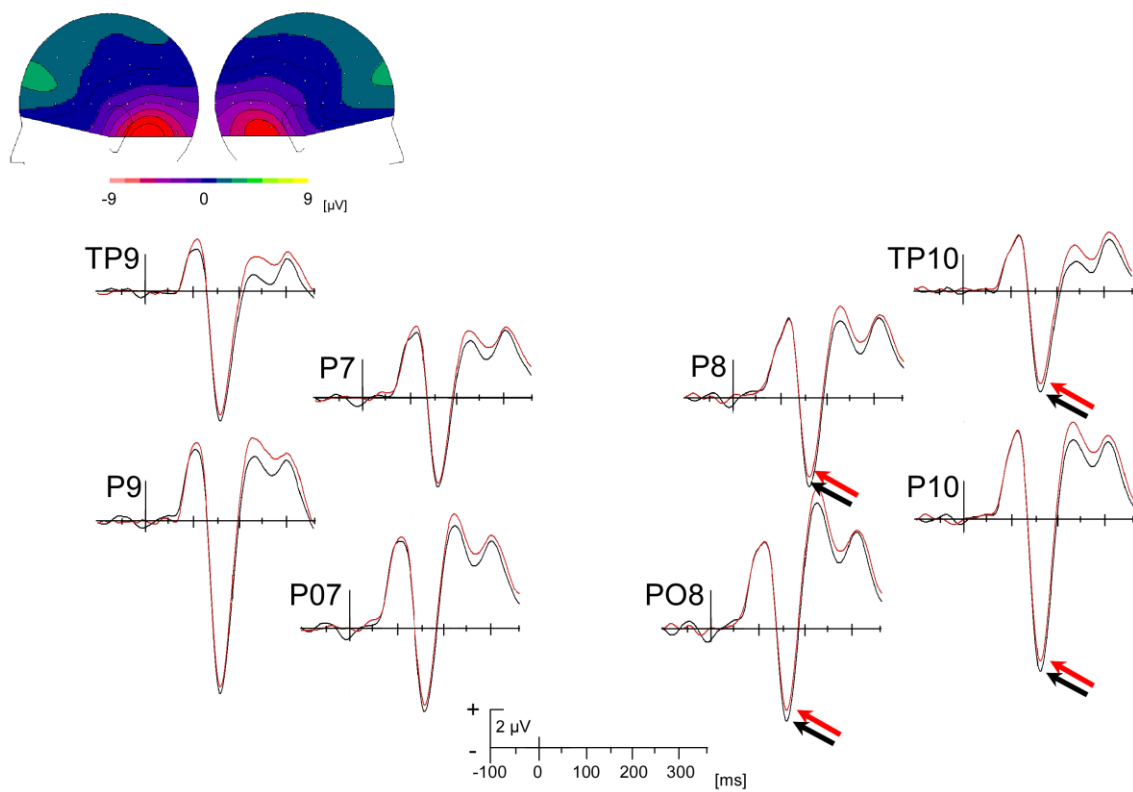
Frontal

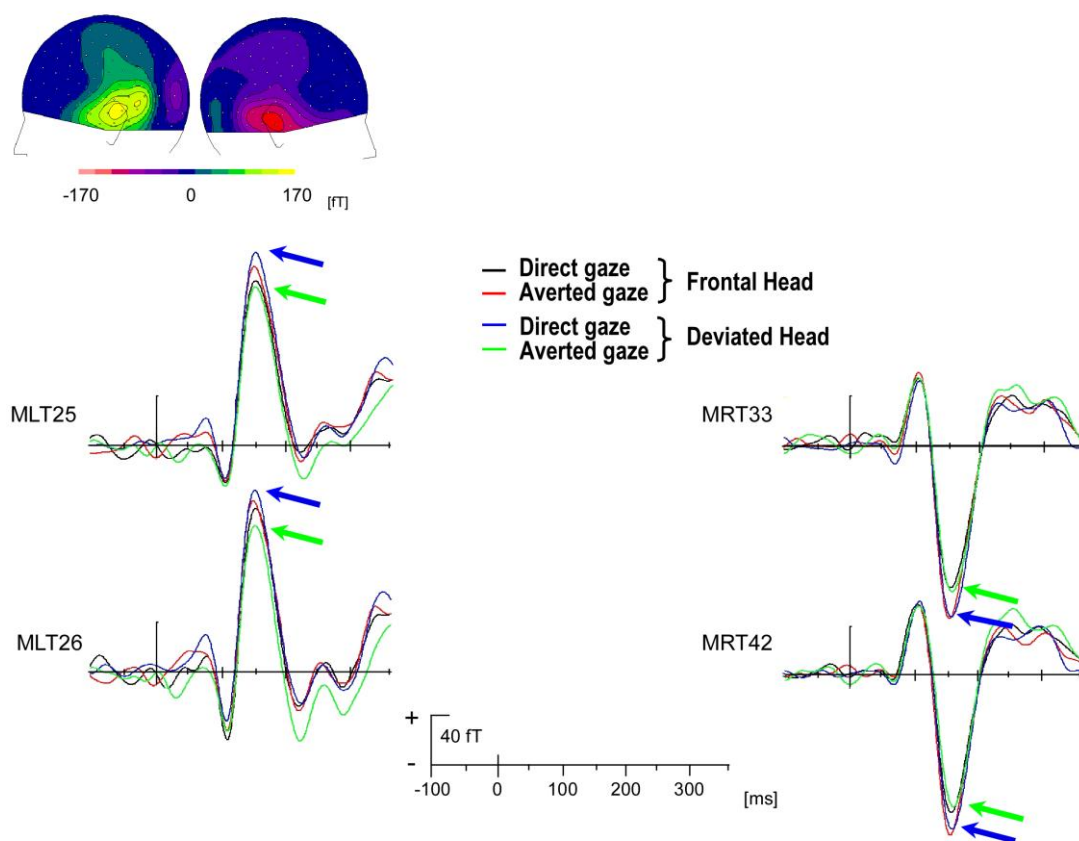


Deviated

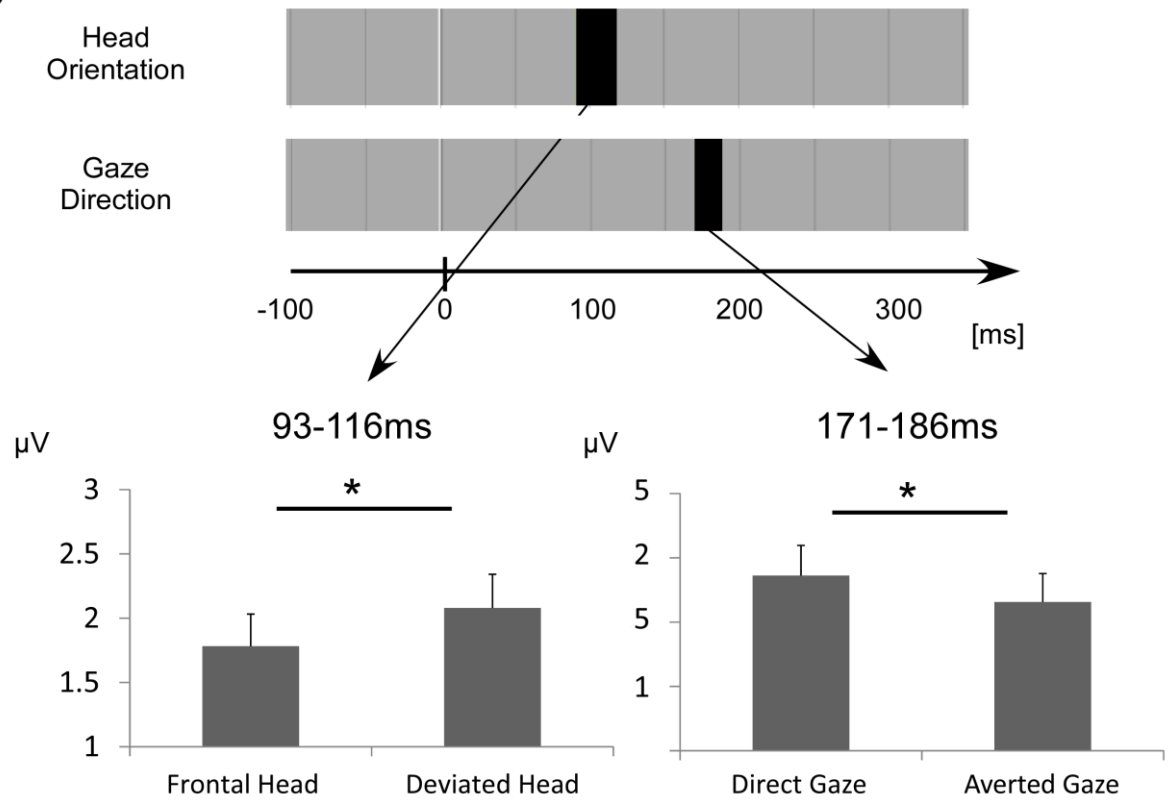




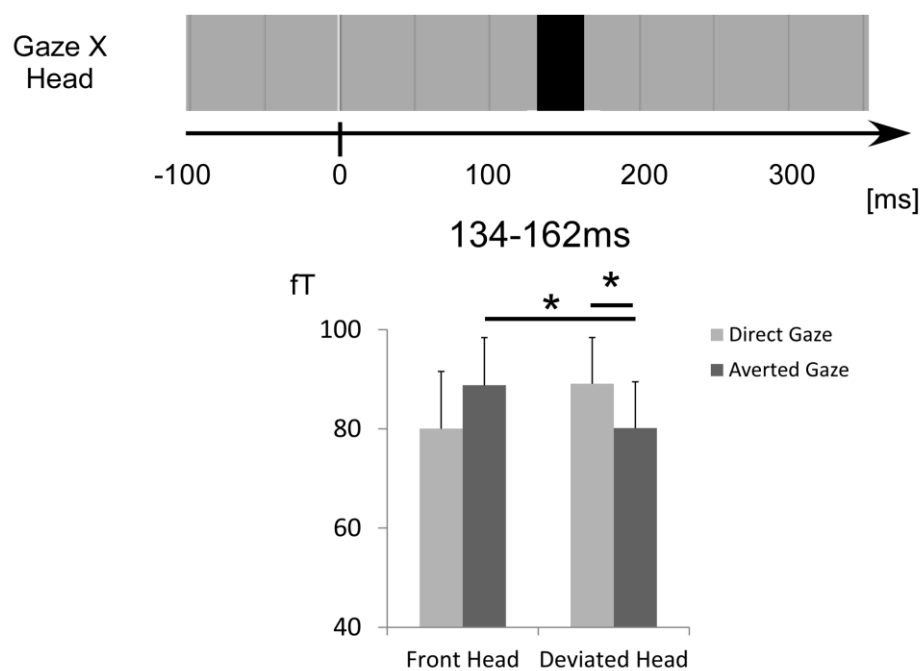


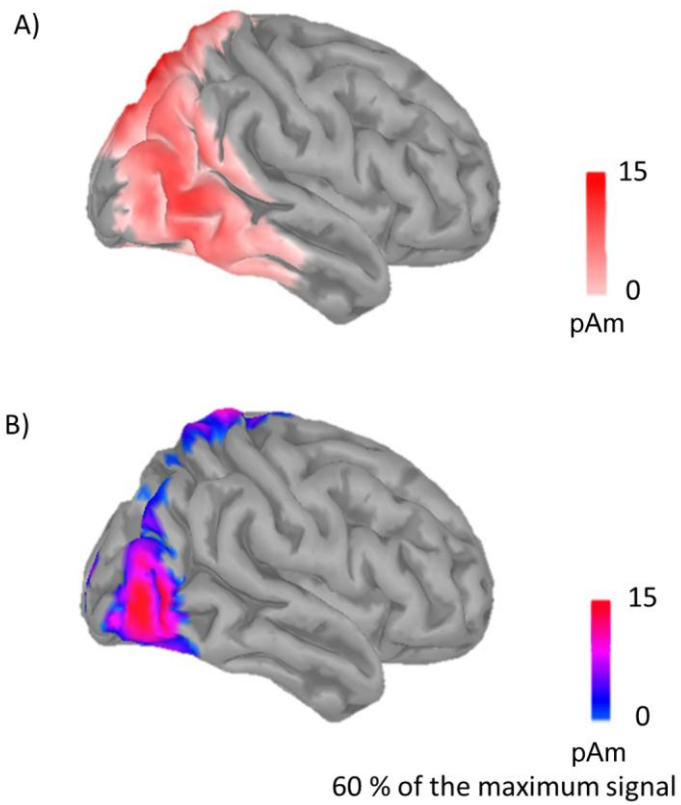


A)

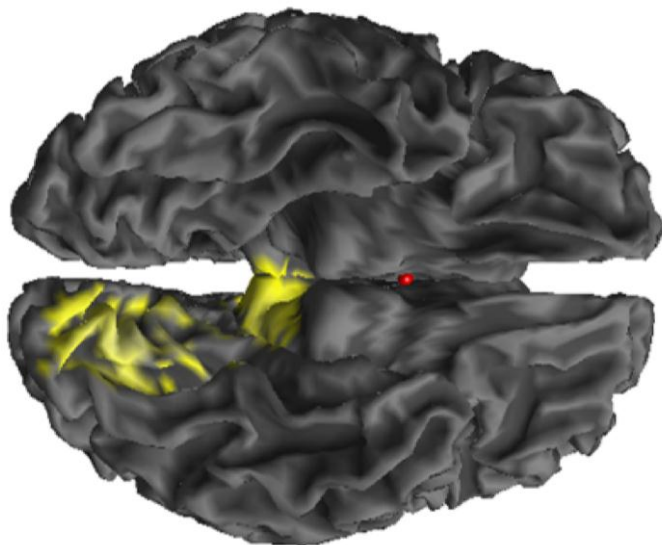


B)

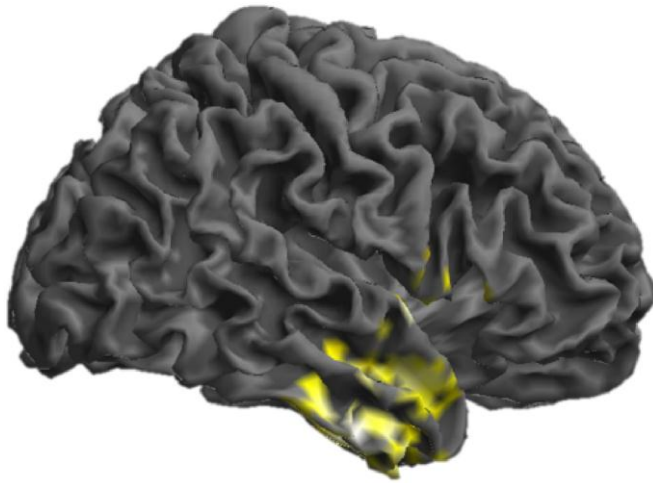




93-116ms



171-186ms



Accepted manuscript

134-162ms

