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When eye creates the contact! ERP evidence for early dissociation between direct and averted gaze motion processing

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Abstract

Direct gaze or eye contact is a strong social signal, which triggers distinct processes as compared to other gaze directions. Thus, direct gaze could be early dissociated from averted gaze during the processing of gaze direction. In order to examine the processing of gaze contact relative to averted gaze, we studied evoked potentials in human adults in response to the apparent motion of gaze. Deviated and frontal faces were presented with a fixed gaze direction, followed by an apparent movement of the eyes either toward the subject or away from him/her. The results showed that the perception of direct relative to averted gaze evoked a greater, later and longer lasting N170, suggesting that gaze contact recruited more resources than averted gaze in the early stage of gaze direction processing. Furthermore, direct and averted motion of gaze elicited distinct ERP components between 160 and 210 ms, initiated over centro-parietal electrodes. Source reconstruction revealed the involvement of the Theory-of-Mind network, including the regions of the superior temporal sulcus, the medial prefrontal and the orbitofrontal cortices, in this early dissociation. In addition, the perception of gaze contact relative to averted gaze yielded increased fronto-central P3a and parieto-occipital P3b. All the results were significant whatever the head orientation. Our findings show that gaze contact, as compared to other gaze directions, is an essential social cue which recruits early specific processes. The dissociation between direct and averted gaze processing occurs as soon as 160 ms, involving the social brain network.

Keywords: Gaze contact; Gaze movement; Evoked potential; Source localisation; Theory of Mind; Social cognition

1. Introduction

Gaze is a crucial cue to decode for adapting one's interpersonal behaviour. Indeed, people's eyes and gaze direction communicate their emotion and their focus of interest in the environment. Thus, decoding others' gaze direction is an essential component and the precursor of the "Theory of Mind" (ToM), namely, the human ability to attribute mental states to other people (Baron-Cohen, 1995). Two main aspects of the perception of gaze direction have been distinguished in the literature: the perception of gaze directed toward the observer (direct gaze or gaze contact) and the perception of gaze directed away from the observer, toward the surrounding space (averted gaze). These two aspects have been shown to involve distinct cognitive processes.

What happens when our interlocutor directs his/her attention toward us? The first function of direct gaze seems to be to inform about the intention of the gazer toward the perceiver. Whereas many species present an aversive response to gaze contact, human primates use this cue together with a large panel of behaviours for communicating and synchronising their interaction with others (Kleinke, 1986; Patterson, 1982). The majority of the pathologies characterized by a social withdrawal (e.g. social phobia, schizophrenia with negative symptomatology, autism) include among their symptoms the avoidance of gaze contact (Greist, 1995; Horley, Williams, Gonsalvez, & Gordon, 2003). These data underline the importance of decoding gaze contact efficiently for well-adapted social interactions and suggests that direct gaze may be early dissociated from averted gaze during the processing of gaze direction.

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Behavioural studies are rich in evidence for the dissociation between direct and averted gaze processing. As for gaze contact, it has been shown that we are highly efficient at detecting direct relative to averted gaze (Conty, Tijus, Hugueville, Coelho, & George, 2006; Senju, Hasegawa, & Tojo, 2005; Von Grünau & Anston, 1995), suggesting that we are biased to detect eye contact. Moreover, perceiving gaze contact can capture visuospatial attention, resulting in delayed orienting of attention toward peripheral cues (Senju & Hasegawa, 2005). Such effect has been attributed to deeper face processing during the gaze contact condition (see Hood, Macrae, Cole-Davies, & Dias, 2003; Vuilleumier, George, Lister, Armony, & Driver, 2005). Likewise, the perception of averted gaze seems to trigger specific processes on its own. It is known to induce an automatic shift of spatial attention toward the gazed-at direction (e.g. Driver, Davis, & Ricciardelli, 1999; Friesen & Kingstone, 2003), which can be observed as soon as at 3 months of age (Hood, Willen, & Driver, 1998). Responding to averted gaze leads very early in development to joint attention, the ability to direct our attention at the same object as our interlocutor (Reddy, 2003). Altogether, these data suggest that the perception of averted gaze triggers processes mainly related to the orientation of spatial attention and joint attention. By contrast, direct gaze triggers preferential detection processes and enhanced allocation of resources to the seen face, affecting cognitive performance. The clear dissociation between the processes elicited by direct versus averted gaze perception raises the question as to when and where responses to direct and averted gaze are dissociated in the brain. Here we used functional brain imaging based on electroencephalography (EEG) and source reconstruction to investigate this question.

While movement appears as an essential component of gaze, a number of brain imaging studies have examined the perception of gaze direction using static face stimuli. They have shown clear dissociation between direct and averted gaze processing which converged closely with the conclusions of behavioural studies. Direct gaze induces increased activation in bilateral fusiform gyrus, a region known to be involved in face encoding (George, Driver, & Dolan, 2001, see also Calder et al., 2002; George et al., 2001; Kampe, Frith, Dolan, & Frith, 2001). Moreover, it activates the amygdala, a structure involved in emotional processing (George et al., 2001; Kawashima et al., 1999; Wicker, Perrett, Baron-Cohen, & Decety, 2003), supporting the idea that direct gaze is emotionally significant even when the gazing face does not express any particular emotion. By contrast, Hoffman and Haxby (2000, Experiment 2) found that the superior temporal sulcus (STS), involved in biological motion processing and social attention processes, and the intraparietal sulcus (IPS), involved in spatial attention processes, showed greater activation for passive viewing of faces with averted compared to direct gaze (see also Puce, Allison, Asgari, Gore, & McCarthy, 1998 using moving stimuli). Furthermore, in a positron emission tomography (PET) study, Calder et al. (2002) showed that the medial prefrontal cortex (MPF), known to be involved in ToM tasks, is engaged in the processing of both direct and averted gaze, but would be primarily involved when viewing averted rather than direct gaze.

While the neural bases of direct and averted gaze processing have started to be uncovered, little is known about the temporal dynamics of these brain responses. Using EEG in human infant, Farroni, Csibra, Simion, and Johnson (2002) studied the N170, an early face-sensitive event-related potential (ERP) elicited on occipito-temporal electrodes and known to reflect face encoding (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003). These authors showed enhanced “infant N170” (around 240 ms) in 4-month-old babies looking at static faces establishing gaze contact. This reinforces the idea that the perception of direct gaze induces deeper face processing. Importantly, these results also suggest that the perception of direct relative to averted gaze may elicit early increased responses in the brain. However, the studies ran in EEG and magnetoencephalography (MEG) in human adult have failed to confirm this hypothesis so far.

Using static face stimuli, Watanabe, Miki, and Kakigi (2002) found a very limited effect of gaze with greater N190 to right averted (relative to straight) gaze on the right T6′ electrode (see also Taylor, Itier, Allison, & Edmonds, 2001). Moreover, several recent EEG and MEG studies have focused on the perception of moving gaze. The first investigators were Puce, Smith, and Allison (2000). When recording ERPs to eye and mouth movements in human adults, these authors found evoked N170 and P350. The N170 was found to be modulated by the direction of gaze movement as it was greater and earlier for gaze directing away from the viewer compared to gaze directing toward him/her. Moreover, using MEG, Watanabe, Kakigi and Puce (2001) did not find any significant effect of gaze direction on the M170. These results stand in contrast with the findings of greater face-encoding related activity in response to direct relative to averted gaze in babies (Farroni et al., 2002). It is possible that the N170 elicited by eye motion originates from different sources and reflects different encoding processes as compared to the N170 elicited by static faces. However, discrepancies in gaze effects have been obtained within, respectively, static as well as dynamic protocols. Alternatively, these discrepancies may originate from a baseline bias in most dynamic protocols. Indeed, a common feature of the EEG and MEG studies on the perception of gaze motion so far has been to use direct gaze as a starting point condition with the eyes then moving sideways (averted motion condition) and returning afterwards to central position (direct motion condition). Such protocol could have biased the data toward eliciting greater brain responses to averted gaze than to direct gaze motion, for direct gaze served as a baseline. In a recent study, Pelphrey et al. (2004) did control for such bias: they used an animated male character who shifted furtively his gaze from a determinate common position, either toward the viewer or away from him/her, with the same movement quantity. Using fMRI, the authors found that direct gaze motion evoked greater STS activity than averted gaze motion did. Such result predicts that the processes related to the encoding of both static and moving gaze may be enhanced by gaze contact. Furthermore, in an EEG study, Senju, Hasegawa, et al. (2005) and Senju, Tojo, Yaguchi, and Hasegawa (2005) used an odd-ball paradigm with a frequent face stimuli glancing downward, and rare stimuli glancing either toward or away from the viewer. With such change in eye direction from a common starting gaze condition, they showed an enhanced N200 for faces establishing gaze contact in typically developed children. Thus, using a common baseline for direct and averted gaze condition seems to favour the observation of the processes triggered during the perception of direct gaze motion (see also Calder et al., 2002; Kampe, Frith, & Frith, 2003).

To the best of our knowledge, no EEG study using symmetric condition between direct and averted motion of gaze, with a common baseline for both gaze conditions, has been run in human adults. Our hypothesis was that under this condition, early increased brain responses elicited by direct relative to averted motion of gaze may emerge in ERPs. Thus, face photographs were presented with a fixed gaze direction, then followed by an apparent movement of the eyes either toward the subject or away from him/her with the same movement quantity. Another important issue concerns the interaction between cues to the direction of attention extracted from gaze and head (e.g. Todorovic, 2006). The previous studies on the perception of gaze movement used faces seen under one orientation only, either frontal (Pelphrey, Singerman, Allison, & McCarthy, 2003; Puce et al., 2000, 2003; Watanabe et al., 2001) or deviated (Pelphrey et al., 2004; Senju, Tojo, et al., 2005). However, there is evidence that incongruent configuration between the gaze direction and the head orientation elicits enhanced brain activity (McCarthy, Puce, Belger, & Allison, 1999; Puce et al., 2000). Thus, it is not clear whether the enhancement of N200 for direct gaze under deviated head view in Senju, Tojo, et al. (2005) study and that of N170 for averted gaze under frontal head view in Puce et al.'s studies (2000, 2003) was not just reflecting the incongruent aspect of the eye direction relative to the head orientation in both protocols. Thus, we used both frontal and deviated head orientations to test for any effect of gaze independent of a specific face view.

We found an occipito-temporal N170 that was modulated by the direction of gaze motion. Namely, this ERP component was greater, later and longer lasting for direct as compared to averted motions of gaze. These effects were found whatever the head orientation. Moreover, between 160 and 210 ms, the direction of gaze motion modulated the brain response over central scalp regions. This modulation overlapped partly with the N170 activity. In order to clarify this phenomenon and identify the brain regions involved, we used source reconstruction. This analysis suggested that the differential processing of direct and averted movement of gaze involved a structured brain network from the prefrontal cortex to the temporal regions, as soon as between 150 and 220 ms. In addition, we report P300 components (fronto-central P3a and parieto-occipital P3b) that were greater for direct than averted gaze motion.

2. Methods

2.1. Participants

Seventeen healthy volunteers participated in the experiment (nine males/eight females). Due to fuzziness and/or bad signal-to-noise ratio, three subjects (two males and one female) were excluded from the final sample. Thus, 14 participants (7 males/7 females) were included in this study (mean age = 24 ± 1 years). All had normal or corrected-to-normal vision, were naive to the aim of the experiment and were right-handed according to an abbreviated version of the handedness inventory of Dellatolas et al. (1988). The subjects gave their written informed consent and were paid €40 for their participation.

2.2. Stimuli

Stimuli consisted of 40 face stimuli (20 men/20 women) which were selected from a database of digitised colour portraits of young adult faces collected by George (see Vuilleumier et al., 2005). All faces had neutral expression and involved individuals unknown to our participants. They were systematically taken under the same lighting and viewpoint conditions, in which the direction of the eyes (straight toward the camera/observer, or averted by 30°) and head position (frontal or rotated by 30° from the camera/observer) varied independently in a 2 × 2 factorial design. To avoid any unintended differences in aspects of the resulting background, the eye region from the averted gaze stimuli was cut and pasted into the very same position within the face photograph used for the direct gaze stimuli, separately for frontal and deviated head orientations (Vuilleumier et al., 2005). For each individual face and each head orientation (frontal and deviated), we created an additional photograph with an intermediate direction of gaze (15°), using a morphing procedure between the photograph with the direct gaze and that with the averted gaze (see Fig. 1A). Such a limited gaze deviation is often perceived as ambiguous, whereas subsequent gaze movement toward or away from the subject disambiguates it clearly. Ulead Morph Studio 1.0 was used for this morphing procedure. We distributed about 35–40 control points on the pupil, the iris, the sclera, the eyelid and the eye outline of each individual eye to calculate the morph of the intermediate eye position. Then, for all stimuli (including the frontal faces with direct gaze; see George et al., 2001 and Vuilleumier et al., 2005), right and left sides of deviation were obtained by mirror-imaging. All stimuli were passed in 256 colours and reduced to a height of 740 pixels while preserving their proportion. The stimuli covered a visual angle of 10.7° vertically and 7.6° horizontally.

2.3. Experimental procedure

The participants were comfortably seated at 1.2 m from the screen, with their eyes at the level of those of the stimuli, in a dimly lit room. An apparent eye movement was created by the consecutive presentation of two photographs on the centre of the screen (17 in. CRT screen, resolution 1024 × 768 pixels). The first photograph was always a stimulus with intermediate gaze direction. It was presented during a random time ranging between 600 and 800 ms, then immediately followed by a second stimulus presenting the same face with the same head orientation but with either direct (50% of the trials), or averted gaze (50% of the trials). Thus, the participants viewed a face in which the eyes moved either toward him/her or away from him/her. The second stimulus remained on the screen during 500 ms, and was followed by a fixation cross presented at the level of the middle of the eyes during 500 ms (Fig. 1B). Each individual face was seen under eight conditions: two deviations (rightward/leftward) by two head orientations (frontal/deviated) by two direction of gaze movement (direct/averted). Thus, for each head orientation, both direct gaze and averted gaze resulted equally from leftward and rightward gaze movement. The resulting 320 trials (40 faces by 8 conditions) were presented in 8 blocks of 40 trials each. In each block, each face appeared under one experimental condition drawn randomly from the eight available conditions, so that each condition was seen five times per block. The eight blocks were presented in a random order, then repeated once in the same order, but with a different order of trials within each block. The order of block presentation was counterbalanced across participants. Trial onset asynchrony was randomized between 3100 and 4300 ms.

2.4. Experimental task

The participant had to detect as accurately and as quickly as possible whether the eyes of the stimulus were directing toward him/her or away from him/her. The participant reported his/her response by a two-choice button press. Half the participants had to press the button under their right index if the gaze was directing toward him/her and the button under their right middle finger if the gaze was directing away from him/her. This assignment was reversed for the other half

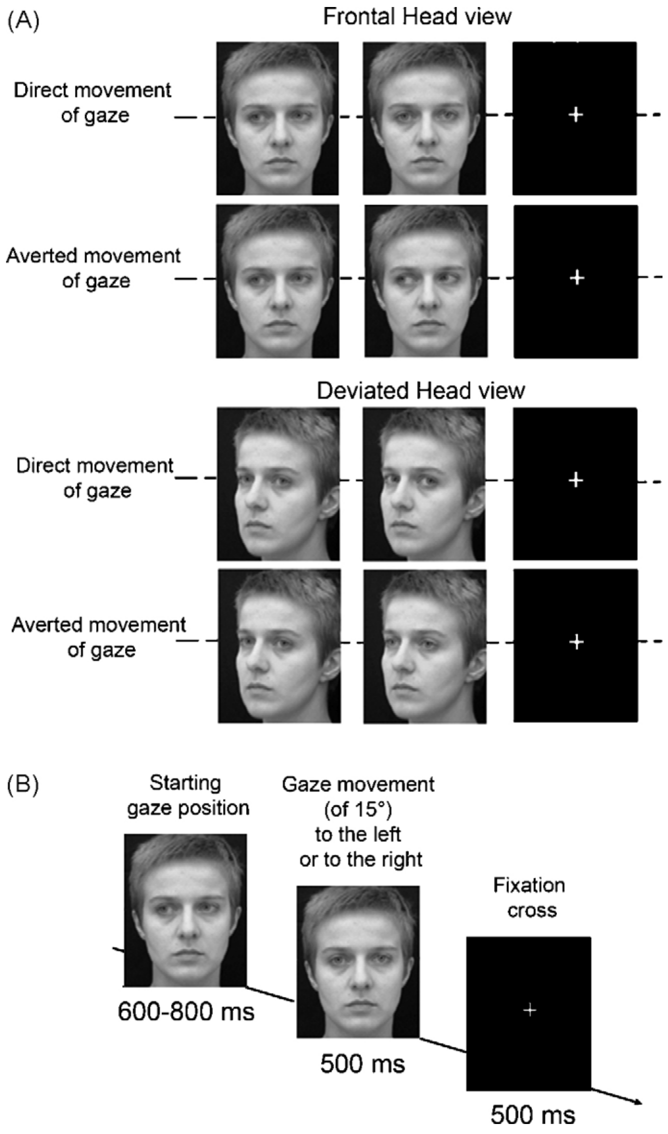

Fig. 1. Experimental design. (A) Example of a face stimulus seen under the four main experimental conditions of gaze motion direction (direct/averted) and head orientation (frontal/deviated). (B) Time course of an experimental trial.

of the participants. In order to limit the eye movements of the participants, they received the instruction to avoid blinking from the onset of the face presentation to the disappearance of the fixation cross. They were also instructed to maintain fixation of the face at about the middle of the eyes and to avoid any horizontal eye movement when the gaze moved. Participants could rest after each block. At the end of the experiment, they were debriefed and thanked.

2.5. *EEG recording*

Continuous electroencephalographic (EEG) activity was recorded with a MICROMED EEG system from 72 electrodes evenly distributed over the scalp, according to the 10/10 extended system, using an ElectroCap (including a row of low occipito-temporal electrodes). Continuous EEG was recorded with respect to a nose reference at a sampling rate of 512 Hz. Electrode impedances were kept under 20 kΩ. The signal was amplified and band-pass filtered online at 0.16–160 Hz. Four facial bipolar electrodes placed on the outer canthi of the eyes and in the inferior and superior areas of the director eye orbit monitored, respectively, horizontal and vertical EOG. Trials containing artefacts were manually rejected. Blinks and vertical eye movements were automatically corrected with a dedicated software developed in our laboratory (Gratton, Coles, & Donchin, 1983). The raw EEG data were then filtered using a 1–30 Hz band-pass filter. Finally, in order to study the ERPs in response to the perception of the eye movement, ERPs were computed for each condition separately between 200 ms before and 1000 ms after the eye movement. In other words, time zero (T_0) was the onset of the second stimulus (creating apparent gaze motion) and the baseline was computed during the presentation of the initial face.

2.6. *Data analyses*

All analyses pooled over rightward and leftward sides of deviation and were conducted using repeated-measures analyses of variance (ANOVA). Planned comparisons were performed for the analysis of simple main effects when interactions were observed. All comparisons with two or more degrees of freedom were adjusted for violations of sphericity with the Greenhouse-Geisser correction. Greenhouse-Geisser epsilons (ε) and p values after correction are reported when appropriate.

2.6.1. *Behavioural data*

The percentage of correct responses (%CR) and mean reaction time of the correct responses (RT) were computed separately for direct and averted gaze motions under frontal and deviated head views. Two-way ANOVAs were carried out with gaze direction (direct/averted) and head orientation (frontal/deviated) as within-subjects factor.

2.6.2. *ERP data*

For each participant, the amplitude and the latency of the N170 maximum peak were measured on a group of six electrodes for which the N170 peak was maximal in all experimental conditions and in each hemisphere. These six electrodes were chosen among CP5/6, P5/6, PO1/2, TP7/8, P7/8, PO7/8, TP9/10, P9/10, and PO9/10 in every subject. They thus varied from one subject to the next, and the latency and amplitude parameters were then pooled over electrodes in each hemisphere and subject. Moreover, for each participant, condition and hemisphere, we picked the electrode on which the N170 was maximal and calculated the two time instants where the wave reached 70% of its maximum amplitude on its rising and decreasing slopes. Then, we calculated the duration of the N170 by subtracting the two latencies obtained. For all the N170 parameters, the ANOVAs were carried out with gaze direction (direct/averted), head orientation (frontal/deviated), and hemisphere (right/left) as within-subjects factor.

Furthermore, we measured the mean amplitude between 160 and 210 ms over the midline centro-parietal (CP1/P1, CPz/Pz and CP2/P2) and right and left lateral occipito-temporal electrodes (TP7/8, P7/8, PO7/8, TP9/10, P9/10 and PO9/10), separately for each experimental condition and each participant. The ANOVA, pooling over electrodes in each scalp region, was carried out with gaze direction (direct/averted), head orientation (frontal/deviated), and scalp region (central/right/left) as within-subjects factor.

Finally, we analysed the P300 components. We computed mean ERP amplitude from 250 to 450 ms over fronto-central electrodes (FC1/C1//FCz/Cz FC2/C2) for P3a and from 300 to 500 ms over parieto-occipital electrodes (PO7/PO1/POz/PO2/PO8) for P3b, separately for each experimental condition and participant. For both components, ANOVAs were then carried out with gaze direction (direct/averted) and head orientation (frontal/deviated) as within-subjects factors.

2.6.3. *Distributed source analysis*

Time-resolved imaging of cortical currents was performed using BrainStorm (freely available at: http://neuroimage.usc.edu/brainstorm) using the regularized weighted minimum-norm estimation (WMNE) approach. This technique has proven being robust to noise in scalp data and head model approximations with fair spatial resolution (Baillet, Mosher, & Leahy, 2001). Amongst the infinite number of possible solutions to the EEG inverse modelling problem, WMNE is the unique solution with minimal overall intensity of cortical currents at each time instant (Michel et al., 2004). The weighting in WMNE further equilibrates the relative contributions of deeper and more superficial sources by normalizing their respective forward fields, thereby reducing the natural bias of basic MNE approaches toward more superficial generators.

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The associated imaging model consisted of 10,000 cortically distributed current dipoles whose locations and orientations were constrained onto the grey matter surface of the BrainStorm generic brain model built from the standard brain of the Montreal Neurological Institute (MNI). Following the procedure used in Sergent, Baillet, and Dehaene (2005), the cortex, bone and scalp surface envelopes were then warped to the standard geometry of the EEG sensor net used in our experiments (see Darvas, Ermer, Mosher, & Leahy, 2006 for technical justifications on the approach). Forward modelling was completed using the analytical EEG solution in the three-sphere geometry with Berg approximation (Berg & Scherg, 1994). Cortical current imaging over the entire time epoch was performed for each condition of gaze motion direction (direct/averted), pooling over head orientation, for each subject and for the grand average of the 14 participants. The current amplitude at each elementary dipole – located at every vertex of the segmented cortical surface – was subsequently transformed into *z*-score with respect to the mean and standard deviation estimated from the baseline period. In the following, “activations” of reconstructed sources are expressed in terms of (estimated) dipole current amplitude (see Sergent et al., 2005 for a similar terminology).

Our analysis focused on the brain network involved in the differential ERP response to direct minus averted gaze observed between 160 and 210 ms. We therefore computed the WMNE of the “direct minus averted gaze” difference for each participant.[1] The time-averages of WMNE currents within seven successive sliding windows of 10 ms duration were computed from 150 to 220 ms. In each time window, only activations extending over at least five vertices, with amplitudes above 50% of the maximal source amplitude and a significance score below $p < .001$ in the t-test for direct versus averted gaze comparison, were considered as significant. Brodmann’s areas (BA) were used as approximate landmarks of these activations from the anatomical labelling of the MNI brain template provided with the MRIcro software (Rorden & Brett, 2000).

3. Results

3.1. Behavioural results

The analysis on RTs showed a significant main effect of gaze direction ($F_{(1,13)} = 11.8$, $p < .01$). The RTs were shorter for the direct compared to the averted gaze motion (see Table 1). An interaction between gaze direction and head orientation was observed ($F_{(1,13)} = 7.6$, $p < .02$), revealing that the gaze effect was more marked under frontal head view (mean difference = 41 ± 11 ms, $F_{(1,13)} = 13.1$, $p < .01$) compared to deviated head view (mean difference = 18 ± 7 ms, $F_{(1,13)} = 5.9$, $p < .04$). Note, however, that the gaze effect was significant whatever the head orientation. These results corroborate a growing number of studies showing that we are biased at detecting direct as compared to averted gaze (Conty et al., 2006; Senju & Hasegawa, 2005; Von Grünau & Anston, 1995).

Moreover, there was also a significant main effect of Head Orientation on RTs data ($F_{(1,13)} = 94.9$, $p < .0001$) with shorter RTs for frontal than deviated head. Together with this effect, the ANOVA on the percentage of correct response (%CR) revealed that the participants were also better at judging the direction of gaze motion when the head was frontal than when it was deviated ($F_{(1,13)} = 22.47$, $p < .001$; Table 1). There was no other significant effect on %CR (all $p > .05$). The effect of Head Orientation on both RT and %CR converges with the finding of greater task difficulty under deviated than frontal head view during gaze processing (Gibson & Pick, 1963).

Table 1
Mean RT and %CR for each condition of gaze direction and head orientation

	Frontal head		Deviated head	
	Direct gaze	Averted gaze	Direct gaze	Averted gaze
RT	470 ± 29 ms	511 ± 30 ms	521 ± 29 ms	539 ± 32 ms
%CR	99.5 ± 0.3	99.1 ± 0.3	96.9 ± 0.7	98.2 ± 0.4

3.2. ERP results

The grand average waveforms from the 14 subjects are shown for all gaze movement conditions on a selection of frontal, central, parietal and occipito-temporal electrodes in Fig. 2. The most prominent deflections were the negative peak of the occipito-temporal N170, followed by the positive peak of the P300.[2] Additionally, activities clearly diverged for direct versus averted gaze conditions between 160 and 210 ms in midline centro-parietal regions (Fig. 2).

3.2.1. N170

The N170 culminated between 155 and 175 ms over the occipito-temporal sites of the scalp in both hemispheres (Fig. 3A). The analysis on N170 peak amplitude showed a significant effect of gaze direction ($F_{(1,13)} = 30.7$, $p < .0001$; see Fig. 3B): the N170 amplitude was greater for direct compared to averted gaze (mean difference: 1.4 ± 0.2 μV). Moreover, the interaction between gaze direction and head orientation was significant ($F_{(1,13)} = 7.1$, $p < .02$.). This reflected that the gaze effect was more marked under deviated head view (mean difference: 1.9 ± 0.3 μV, $F_{(1,13)} = 38$, $p < .0001$) than under frontal head view (mean difference = 0.8 ± 0.3 μV, $F_{(1,13)} = 6.9$, $p < .03$). However, it was significant whatever the head orientation. There was no significant effect of Head Orientation ($F < 1$), nor of Hemisphere ($F_{(1,13)} = 2.8$, $p > .10$).

Furthermore, the N170 peak was delayed for direct compared to averted gaze (mean difference = 8 ± 2 ms, $F_{(1,13)} = 22.7$, $p < .0001$; see Fig. 3B). The N170 peaked also slightly later in the right than the left hemisphere (mean difference = 3 ± 1 ms, $F_{(1,13)} = 8.8$, $p < .02$). No significant effect of Head Orientation was observed on N170 latency ($F < 1$).

Finally, the analysis on N170 duration showed a significant effect of gaze direction ($F(1,13) = 3.2$, $p < .03$): the N170

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[1] The WMNE is a linear inverse source model and the same value for the regularization parameter was used across conditions and subjects, which does not introduce any non-linearity in the approach. The only – though limited – source of non-linearity in data processing may have arisen from the normalisation of source activity using a *z*-score. We checked that this did not introduce any non-linearity before mapping sources from the ERP difference between direct and averted gaze conditions. Indeed, sources were first estimated separately for both conditions and for each subject and we verified that the WMNE of the difference was identical to the difference of the WMNEs.

[2] We noted the presence of a slow negative drift over the posterior regions, which was not fully filtered out by the 1 Hz high-pass filter. Examining the ERP averages in response to the initial face showed that this was attributable to a contingent negative variation (CNV) activity, which was not fully cancelled by the jitter introduced between the face onset and the eye movement. However, importantly, this CNV-like drift was equivalent in every condition of eye movement direction and head orientation, as can be seen in Fig. 4.

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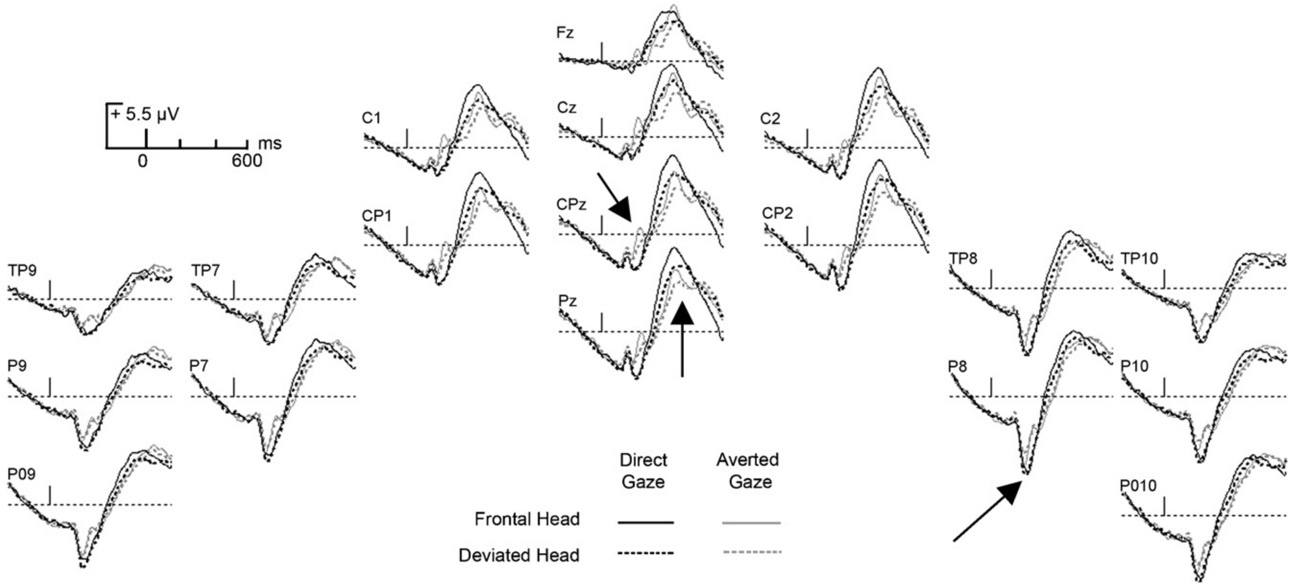

Fig. 2. Grand average ERP waveforms from the 14 subjects under each condition of gaze direction and head orientation. The ERP time course is shown on a subset of 16 electrodes. The zero time point corresponds to the gaze movement. The four experimental conditions examined were direct gaze movement under frontal (in plain black line) and deviated head view (in dotted black lines), and averted gaze movement under frontal (in plain grey line) and deviated head view (in dotted grey line). All conditions elicited N170 (indicated by an arrow at electrode P8) and P300 components (indicated by an arrow at electrode Pz). Toward 200 ms, averted gaze conditions elicited a positive evoked response over fronto-centro-parietal regions, whereas direct gaze conditions elicited a negative potential (indicated by an arrow at electrode CPz).

lasted longer for direct compared to averted gaze (mean difference = 10 ± 4 ms; see Fig. 3B). The ANOVA did not revealed any other effect or interaction on N170 duration (all $F < 2$, all $p > .10$).

3.2.2. *Mean amplitude between 160 and 210 ms*

The inspection of the grand average ERP (Fig. 2) showed that direct and averted gaze conditions yielded clearly divergent activity in the early time range. The examination of the global “direct minus averted gaze” ERP difference showed that this differential activity culminated first over centro-parietal regions (around 185 ms) and extended later on over left and right occipito-temporal regions (around 193 and 196 ms, respectively; see Fig. 4), overlapping the N170 response. To characterize this effect further, we analysed the mean amplitude between 160 and 210 ms over centro-parietal and occipito-temporal regions. The analyses confirmed that direct gaze induced more negative activity than averted gaze between 160 and 210 ms (mean difference = 2.0 ± 0.3 µV, $F_{(1,13)} = 41.0$, $p < .0001$). This effect was of the same order of magnitude and significant on centro-parietal as well as on occipito-temporal Scalp Regions (all $p < .001$; Fig. 4). Furthermore, there was a local effect of Head Orientation restricted to the central scalp region: in this region, frontal head view induced more positive activity than deviated head view during averted gaze processing only (mean difference = 1.0 ± 0.4 µV, $F_{(1,13)} = 6.6$, $p < .03$; the interactions between head orientation and scalp region, and between gaze direction, head orientation and scalp region were significant, both $p < .02$). Taken together, these results support the existence of an additional process, different from the N170 activity, which emerged on centro-parietal region and extended on occipito-temporal regions.

3.2.3. *P300*

The P300 was observed between 220 and 600 ms over fronto-central (P3a) and parieto-occipital (P3b) regions. The mean amplitude of the P3a wave, measured between 250 and 450 ms, showed a significant main effect of gaze direction: P3a amplitude was greater for direct compared to averted gaze ($F_{(1,13)} = 9.1$, $p < .01$; Fig. 5). P3a amplitude was also greater for frontal compared to deviated head view ($F_{(1,13)} = 8.3$, $p < .02$). No interaction between Gaze direction and Head Orientation was observed ($F < 1$).

Moreover, the mean amplitude of the P3b, measured between 300 and 500 ms, was greater for direct compared to averted gaze ($F_{(1,13)} = 5.6$, $p < .04$; Fig. 5). There was also a trend to greater P3b for frontal than deviated head ($F_{(1,13)} = 3.9$, $p = .07$). No interaction between Gaze direction and Head Orientation was observed ($F < 1$).

3.3. *Source localisation*

We focused on the brain network involved in the dissociation between direct and averted gaze conditions observed in the 160–210 ms time window. To this aim, we examined the sources of the “direct minus averted gaze” difference. We focused on the mean source activity in successive sliding windows of 10 ms duration from 150 to 220 ms and examined the source significantly involved in each time window. This revealed the involvement of a spatially and temporally structured network (Fig. 6). There was a first cluster of activation in the right and left superior dorso-medial prefrontal regions (BA 8/9; Fig. 6, cluster A). This activation was seen as soon as from 150 to 160 ms, and remained significant until 210–220 ms. It extended into more lateral dorsal frontal regions (BA 8/9) from 170–180

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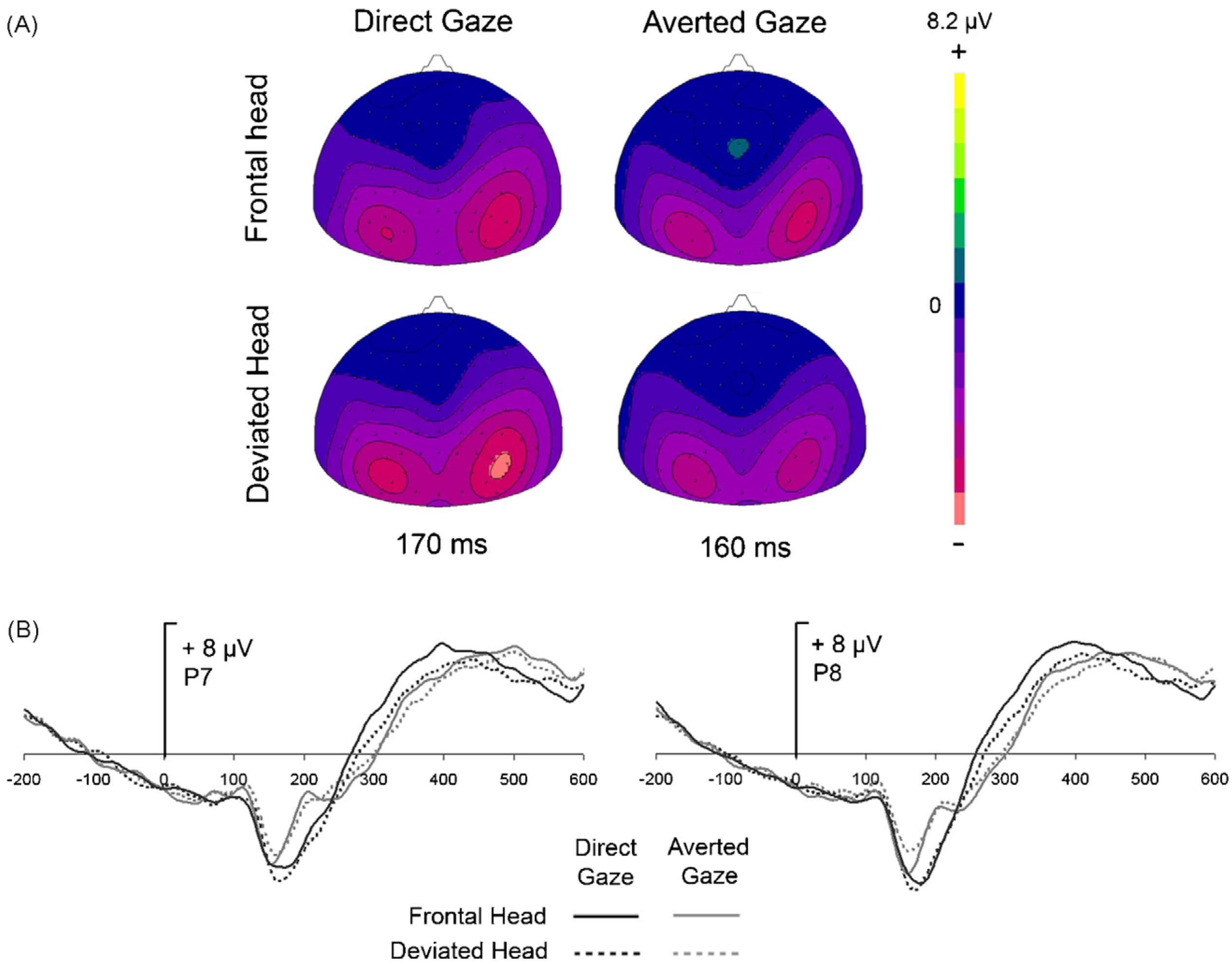

Fig. 3. N170 scalp distribution and time course in each condition of gaze direction and head orientation. (A) Scalp potential maps at the time of the N170 peak (170 ms for direct gaze conditions, vs. 160 ms for averted gaze conditions) for the four experimental conditions. The maps are represented over large top head views. (B) N170 time course in the four experimental conditions over one electrode of the left hemisphere (P7) and one electrode of the right hemisphere (P8). The N170 was increased, delayed and longer lasting for direct (black traces) compared to averted gaze conditions (grey traces).

to 200–210 ms, particularly in the right hemisphere where it extended into BA 6 (Fig. 6, cluster B). Moreover, from 180 to 190 ms, a cluster of sources in the orbitofrontal region was seen, which showed sustained activation (at least in the left hemisphere) until 210–220 ms (Fig. 6, cluster C). From 190 to 200 ms, significant clusters in the right lateral temporal region (BA 21/22) centred on the STS region were observed (Fig. 6, cluster D). This activation extended to the ascendant part of the right STS (BA 39) between 200 and 210 ms. As can be seen in Fig. 7, only the first early bilateral dorso-medial prefrontal cluster showed greater activation for averted than for direct motion of gaze. In all other regions the perception of direct motion of gaze yielded significantly more activation than the perception of averted motion of gaze did.

4. Discussion

Our objective was to examine the temporal dynamics of the perception of direct and averted gaze motion. Using EEG, we showed that the perception of a gaze directing toward the subject, as compared to the perception of a gaze directing away from the viewer, yielded greater, later and longer lasting occipito-temporal N170. Moreover, the direction of gaze motion influenced the mean amplitude of ERP responses between 160 and 210 ms starting over centro-parietal electrodes and extending into occipito-temporal regions. Source reconstruction revealed a temporally and spatially structured brain network from the dorsal prefrontal to the lateral temporal regions involved in the early differential responses to gaze contact versus averted gaze. In addition, direct relative to averted gaze elicited greater P3a and P3b. Although some of these effects were modulated by head orientation, all were found significant under both frontal and deviated head views.

4.1. *Gaze effects in the early time range*

In agreement with former studies, we observed a N170 elicited by the perception of eye motion (Puce et al., 2000, 2003). Moreover, the analyses revealed significant effect of gaze direction on different N170 characteristics: its amplitude was larger, its latency increased, and its duration longer for direct compared to averted gaze motion. These results do not converge fully with

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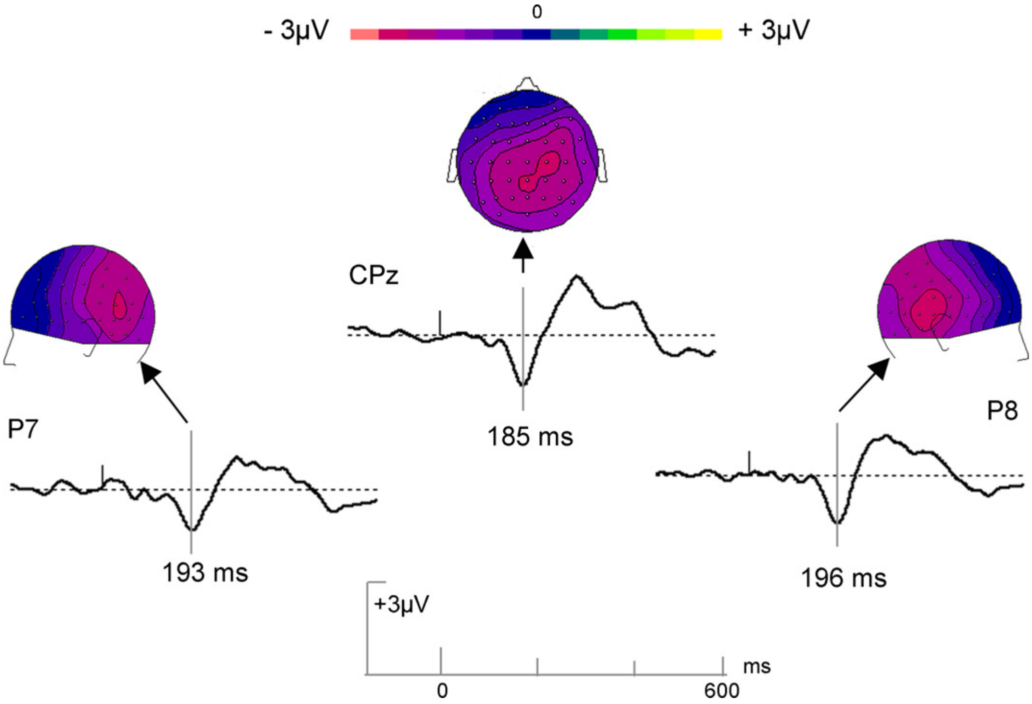

Fig. 4. Grand average ERP difference for direct minus averted gaze conditions. The time course of the ERP difference averaged over head orientation is illustrated at three representative electrodes from each region of measurement (CPz in centro-parietal region, P8 and P7 in the right and left temporal hemispheres, respectively). The scalp distribution at the time of the early difference peak is presented above each time course. The ERP difference culminated initially over the centro-parietal region at 185 ms, while it peaked over bilateral occipito-temporal regions around 195 ms.

those of Puce et al. (2000) who showed a later, but smaller N170 for direct versus averted motion of gaze (see also Watanabe et al., 2001). However, as mentioned in Section 1, these studies used a single face stimulus presented with a direct gaze as baseline, before the eyes moved sideway (averted gaze condition), and then returned in central position (direct gaze condition). It is thus possible that repetition effects may have contributed to reducing the response to direct gaze stimuli while the new configuration of the eyes induced enhanced response to averted gaze. Furthermore, it may have reduced the social relevance of direct gaze, thus causing the greater N170 in the averted relative to direct gaze conditions. Hence, in our experiment, when using an intermediate eye position as a common baseline for direct and averted gaze movement in a variety of faces, we found a greater, later and longer lasting N170 for direct motion of gaze, as compared to averted motion of gaze.

The result of greater N170 for direct than averted gaze perception is in line with previous studies which found greater face-encoding activities during direct gaze perception but – in their case – using static faces, with EEG in human infants (Farroni et al., 2002) and fMRI in human adults (George et al., 2001). In our experiment, as the face was present before

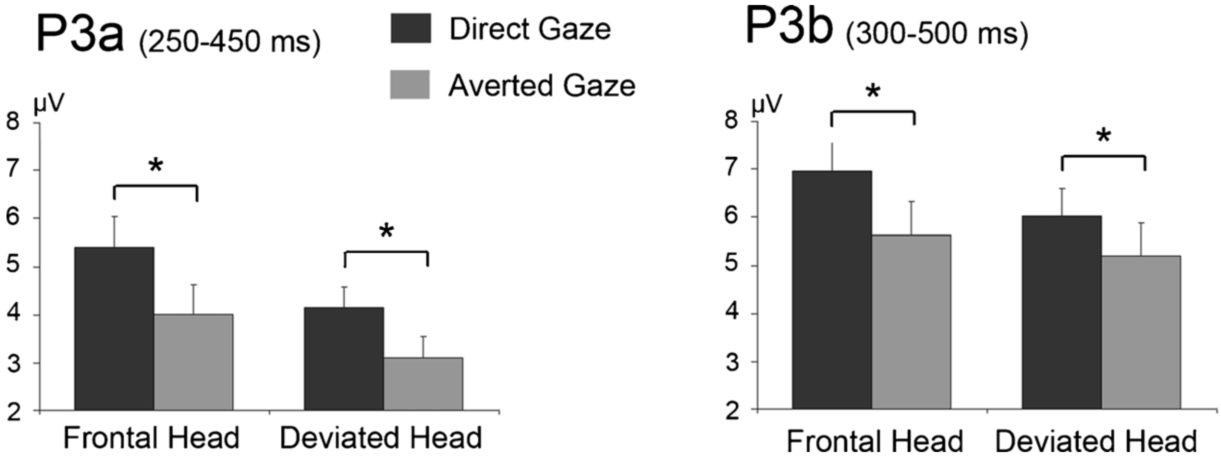

Fig. 5. Effects of gaze direction and head orientation on P3a and P3b amplitudes. Left panel represents mean P3a amplitude (in μV) between 250 and 450 ms in the four experimental conditions of gaze direction and head orientation. Right panel represents mean P3b amplitude (in μV) between 300 and 500 ms in the same conditions. In both plots, direct gaze conditions are represented in black bars, and averted gaze condition in grey bars. Vertical lines above the bars represent the standard error of the mean.

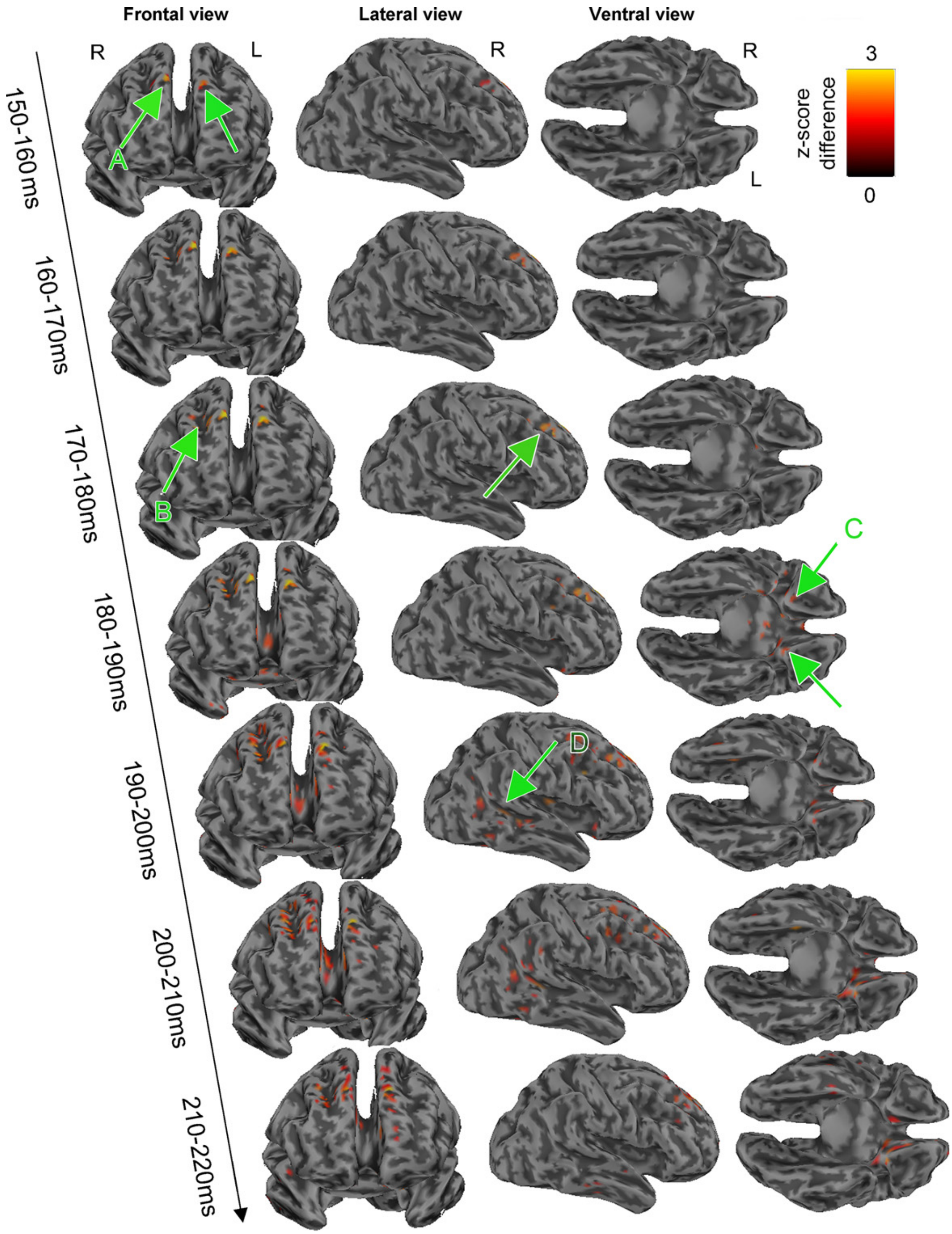

Fig. 6. Differences in source activities between direct and averted gaze conditions from 150 to 220 ms after eye motion. Source activities were averaged in seven 10 ms time windows (presented in raws). In each time window, the absolute mean value of the difference of source activity in *z*-score units is colour-coded and superimposed on an inflated brain template. Only difference reaching 50% of the maximum differential activity within each time window, exceeding $p < .001$, and comprising at least 5 vertices are displayed. Frontal (left column), right (middle column) and bottom (right column) views of the brain are presented. Four main clusters of activation were observed in the superior dorsal prefrontal regions (cluster A from 150 to 160 ms and cluster B from 160 to 170 ms), in the orbito-frontal regions (cluster C from 180 to 190 ms) and in the right lateral temporal regions around the STS (cluster D, from 190 to 200 ms).

its eyes moved, this may mean that direct (relative to averted) gaze triggers an automatic re-encoding of the face or renewed attention to it. Alternatively, the N170 effect may be attributed to biological motion processing, converging with Pelphrey et al. (2004) who showed greater STS activation during the perception of direct motion of gaze in fMRI. In any case, these processes would be enhanced under direct as compared to averted motion of gaze. Moreover, Miyoshi, Katayama, and Morotomi

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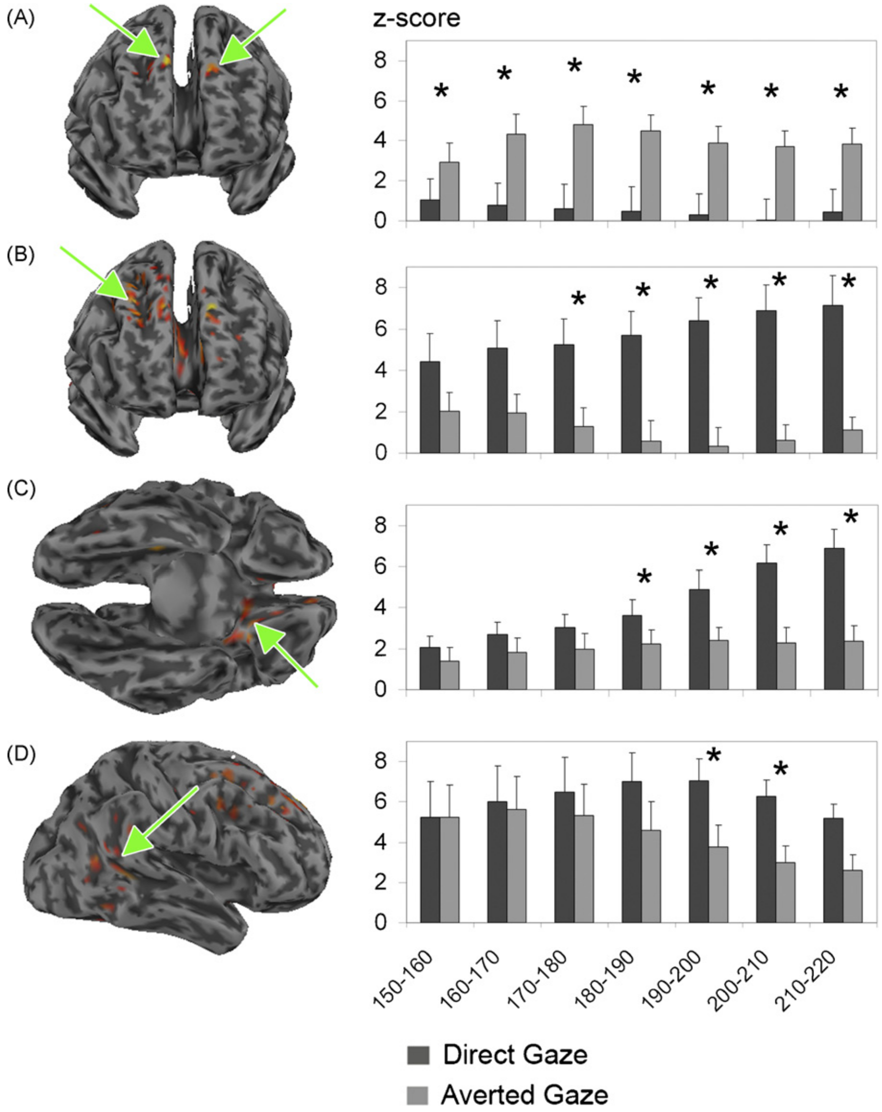

Fig. 7. Source activities for direct and averted gaze conditions in the four clusters of differential activity obtained between 150 and 210 ms (clusters A–D; see Fig. 7). For each cluster, we plotted the activity of the vertex that showed the maximal effect of gaze direction. Bar plots represent the absolute value of this activity (in *z*-score) in the direct (black bars) and averted (grey bars) gaze conditions. Vertical lines above the bars represent the standard error of the mean. In each plot, asterisks mark the 10-ms time windows in which the difference between direct vs. averted gaze conditions was significant for the cluster.

(2004) have shown that the N170 may be modulated by the emotional significance of the stimulus, using changes in the emotional expressions of faces (see also Campanella, Quinet, Bruyer, Crommelinck, & Guerit, 2002). Thus, in our protocol, the greater N170 for direct gaze motion may also be related to the emotional relevance of gaze contact. The increased effect of gaze contact under deviated head view is consistent with this idea, as direct gaze appears more salient under this configuration (Conty et al., 2006; Vuilleumier et al., 2005).

Furthermore, the N170 peaked later for direct than averted motion of gaze. This converges with Puce et al. (2000) latency result for frontal face stimuli and extends it to both frontal and deviated head views as this result was here obtained independently of head orientation. In addition, this latency effect was concomitant with a longer lasting N170 for direct than averted gaze conditions and both these effects seemed closely associated. Namely, the N170 appeared to onset at the same time under all experimental conditions, but direct gaze motion seemed to induce a greater accumulation of the underlying neuronal activity (see Perrett, Oram, & Ashbridge, 1998), thus the N170 reached its peak later, and lasted longer, under the direct than the averted gaze condition. However, it is in fact difficult to decide whether the effect of gaze on latency and duration may be mainly attributed to the direct or to the averted gaze condition. It is possible that averted gaze triggered early and short-lasting N170 because it elicits automatic shift of attention toward the surrounding space thus diverting attention from the face or interrupting the processing of the face per se. On the other hand, direct gaze captures attention onto the face (Senju & Hasegawa, 2005) and ought to trigger deeper processing of the facial context to decode the meaning of gaze contact (Mason, Hood, & Macrae, 2004; Vuilleumier et al., 2005), which may have contributed to the later and longer lasting N170 for direct than averted gaze. In any case, these results show that direct gaze relatively to averted gaze triggers enhanced processing of the face and/or the eye movement. Altogether, our N170 results support the idea that direct gaze represents a greater source of information to extract, mobilizing more resources than averted gaze in the early stage of face and/or motion processing.

Furthermore, direct versus averted gaze conditions yielded additional modulation of ERPs between 160 and 210 ms, culminating over centro-parietal electrodes around 185 ms and then extending over occipito-temporal regions around 195 ms. The centro-parietal activity was further modulated by head orientation under the averted gaze condition. The latter result corroborates the idea that the detection of averted gaze, compared to that of direct gaze, is markedly dependent on head orientation (see Conty et al., 2006). Moreover, these results suggest that additional processes, initially reflected at the central scalp region, occurred during the N170 temporal activity. This is in line with Senju, Tojo, et al. (2005), who found an occipito-temporal N2 component greater for direct compared to averted gaze perception which was clearly distinct from the N170 activity, in typically developed children. Admittedly, the mean gaze effect over occipito-temporal electrodes between 160 and 210 ms cannot be dissociated from the gaze effect on N170 peak in our study. However, the finding of a concomitant early centro-parietal peak of the gaze effect suggests that the difference in brain responses between direct and averted gaze was not limited to a temporal N170 effect. The results obtained with source analysis converged with this interpretation.

4.2. Source localisation

The analysis of the brain regions responsible for the gaze effect between 150 and 220 ms showed a temporally structured brain network, involving first the dorsal prefrontal regions and then extending into the orbito-frontal and STS regions.

In line with previous studies, we found a modulation of activity around the STS region by the direction of gaze motion. Our result showed that this region was significantly more active during direct than averted gaze processing, between 190 and 210 ms. This may appear contradictory with Hoffman and Haxby (2000, Experiment 2) finding of greater STS activation for faces with averted as compared to direct gaze. However, in their design, the averted gaze condition implicated in fact changes between right and left directions of gaze, while there was no such change in the direct gaze condition. This may have confounded Hoffman and Haxby's (2000) result on STS activation. By contrast, our finding of greater STS activity during direct relative to averted gaze perception converged with the result of Pelphrey et al. (2004) who used a common starting eye position for direct and averted movement of gaze as in the present study. Here, we replicated this fMRI result using source reconstruction of scalp ERPs and provided further information about the timing of the STS region involvement. Our result showed that as soon as 190–200 ms the STS differentiated direct and averted gaze stimuli. This difference can be interpreted as greater resource allocation to the processing of direct motion of gaze. The STS is known to be involved in eye motion processing. It has been further shown to be implicated in the processing of cues signalling the direction of social attention (Allison, Puce, & McCarthy, 2000; Perrett et al., 1990, 1985; Puce & Perrett, 2003; Puce et al., 2003) and in ToM processes (Baron-Cohen, 1995; Happe et al., 1996). Thus, the early greater activity of STS region for direct relative to averted gaze perception suggested that more processes of social attention were engaged by direct gaze motion.

Our STS source seemed to be lateralized to the right hemisphere. Such right hemispheric lateralization is consistent with the idea that the right hemisphere is specialized in the processing of facial cues (e.g. Kingstone, Friesen, & Gazzaniga, 2000; Pelphrey et al., 2004; Puce et al., 2000; Watanabe et al., 2001; Wicker, Michel, Henaff, & Decety, 1998). The reason why the STS source modulation by gaze direction was here right lateralized, whereas no equivalent lateralization was observed in the scalp data, is unclear. Source localisation operates a deconvolution of the data and it was here performed on a common cortical surface template as we did not have access to the individual brain anatomy of our subjects. This may have resulted in a loss of sensitivity with only the most overlapping sources reaching the threshold for significance used in this study. This would then suggest that the right sources might have been less variable and/or more overlapping than the left ones.

Furthermore, source localisation revealed a significant early implication of superior dorsal prefrontal regions in the differential processing of direct and averted gaze motion. Sources in these regions were observed between 150 and 220 ms with a functional dissociation between two main clusters of activation. The first one showed a modulation by gaze direction from 150 to 160 ms and was more active during averted than direct gaze motion processing. The second one was active slightly later and showed greater activity for direct than averted gaze motion perception. It should be reminded that the limited resolution of the source localisation undertaken in the present study does not allow deciding to what extent these clusters were actually anatomically distinct. However, this source result corroborated the scalp data which showed clearly divergent activity for direct and averted gaze conditions between 160 and 210 ms over centro-parietal electrodes. Thus, the temporal dynamic of the source activation clearly dissociated between two functional regions in the superior dorsal frontal region.

These regions encompass the dorso-medial prefrontal region (MPF) which has been shown to be involved in the processing of both direct and averted gaze, with PET. (Calder et al., 2002). Previous authors have proposed that the MPF is involved in the representation of the mental states of the self which are used when inferring another person's thought and intentions (Frith & Frith, 1999). According to Calder et al. (2002), the activation obtained during both direct and averted gaze processing in MPF region could reflect different types of ToM processes triggered by the two gaze directions. Under direct gaze, the focus of the other's attention is clearly the observer, thus providing information about the relationship between others and the self. By contrast, averted gaze informs about the relationship between others and the surrounding space. This is consistent with the two opposite response patterns to direct versus averted gaze obtained here around this region. Our results further show that these distinct MPF responses are triggered very early during gaze

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motion perception. Furthermore, the cluster of activation that showed greater activity for direct than averted gaze motion also encompassed more lateral regions in the right hemisphere. These regions include pre-motor areas that are implicated in planning behavioural responses (Heekeren, Marrett, Ruff, Bandettini, & Ungerleider, 2006). Thus, as direct gaze initiates social interaction (Kleinke, 1986), it may be suggested that its perception elicited some propensity to act toward the other. The current design may have favoured the emergence of such propensity and of the associated behavioural planning during direct gaze perception (for example, inducing more active fixation of the seen face). By contrast, the kind of action which may be elicited by the perception of averted gaze is likely to have been inhibited in our study by the instruction to avoid any gaze movement.

Finally, we found a differential source activity under direct versus averted gaze condition in the region of the orbito-frontal cortex. This region showed greater activity for direct than averted gaze perception between 190 and 220 ms. The orbito-frontal cortex is known to be involved in emotional processing (Rolls, Hornak, Wade, & McGrath, 1994). Thus, the greater activation of orbito-frontal cortex for direct gaze processing converged with previous studies that have shown enhanced emotional processing during direct gaze perception (George et al., 2001; Kawashima et al., 1999; Wicker et al., 2003). In addition it is interesting to note that the STS and the orbito-frontal cortex are part of a three components circuit (with the amygdala) underlying the mindreading system (Baron-Cohen, 1995; Happe et al., 1996). Furthermore, the MPF cortex and the STS are known to be linked by direct connections (Ban, Shiwa, & Kawamura, 1991). Thus, overall, source reconstruction revealed a structured circuit involved in ToM processes. Lesion studies have suggested that such circuit is critical for social information processing (Pears, Parkinson, Hopewell, Everitt, & Roberts, 2003). The strong activation of the ToM network during direct gaze processing underlines the importance to decode gaze creating eye contact for social behaviour and the complex nature of such signal. Moreover, source reconstruction allowed us to reveal that this circuit is involved very early on during gaze processing, as soon as from 150 to 220 ms.

4.3. P300

Direct gaze elicited greater P3a and P3b than averted gaze did. We observed also that frontal head orientation yielded greater P3a than deviated head did with a tendency to greater P3b as well. Such effects have not been reported before (Senju, Hasegawa, et al., 2005; Senju, Tojo, et al., 2005). However, as mentioned above, Puce et al.'s (2000) protocol did not favour the observation of the processes yielded by the perception of direct gaze motion. Furthermore, Senju, Hasegawa, et al. (2005) and Senju, Tojo, et al. (2005) used an oddball paradigm which is known to strongly modulate the P300 components. The effect of gaze direction may have been hidden by the rareness of both direct and averted gaze stimuli presentation in their protocol.

Although P3a and P3b are both P300 components elicited in discrimination tasks, they are known to reflect different cognitive processes involved in such tasks (Hansenne, 2000a, 2000b). Mainly, the P3a is described as reflecting a pre-attentional orienting reflex, whereas the P3b amplitude is known to be modulated by the emotional aspect of the stimulus (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Eimer & Holmes, 2002). Thus, our data showed that the perception of both direct gaze and frontal head induced stronger capture of the observer attention and greater emotional processes than, respectively, the perception of averted gaze and of deviated head. These effects are likely to stem from the cues of social attention directed toward the observer that both direct gaze and frontal head constitute.

5. Conclusion

In conclusion, all our results converge to show that gaze contact is a rich source of information which recruits more processing resources than other gaze directions do. Such resource mobilisation is associated with early dissociation of brain responses during direct and averted gaze perception. This dissociation occurs as soon as 150 ms within the ToM brain network. It would subtend the efficient detection of gaze contact and the resulting adaptation of one's social behaviour.

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