Facing the gaze of others
Le regard de l’autre

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Summary Others’ gaze constitutes a rich and essential social signal, which is decoded by taking into account other aspects of the face as well as the social context. Since the perception of averted gaze and that of direct gaze trigger distinct cognitive processes, the studies on gaze perception have focused separately on these two gaze directions. The perception of averted gaze induces orienting of spatial attention in the gazed-at direction as well as joint attention processes while direct gaze or gaze contact signals interest directed at the observer’s self and is often the preliminary to interindividual interactions. Studies in cognitive neuroscience have focused first on averted gaze perception. However, recent studies have emphasised the asymmetries in the processing of direct versus averted gaze. This has led to a growing interest in the neural substrates of direct gaze perception. This issue has recently started to be actively addressed in our group using fMRI, MEG, EEG and source reconstruction methods. These studies emphasise that the perception of direct gaze elicits early processes that are related to face and eye movement encoding as well as to emotion and theory-of-mind.

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Introduction

The face constitutes an essential vehicle of communicative social signals. It conveys information about others’ identity, gender, emotional state, intentions and even personality traits [1,2]. Within the face, the eyes are among the first and most frequently fixated regions [3] and gaze plays a central role in interindividual interactions. It constitutes an active information gathering channel yet also an essential signal for others to decode. Gaze marks things out, hence its perception allows one knowing what is designated by another agent. It gives invaluable indication on the intentional and emotional states of other individuals. While research on the functions of gaze has been developed in social psychology for long [4], the studies on these cognitive processes and brain mechanisms that are associated with the perception of gaze direction are more recent in the field of cognitive neuroscience.

These processes take place automatically and effortlessly in normal individuals. By contrast, they appear altered in autism, thus leading to the difficulty of autistic patients in inferring others’ intentions or desires from eye gaze. More generally, the deficits in the processes associated with gaze perception seem to be linked to the social withdrawal as well as to the impairment in theory of mind, which characterise autistic people, and these deficits may also underlie the abnormal language acquisition observed in many of these patients [5,6]. This suggests that gaze processing plays a central role in the development of social cognition [7]. Thus, this author proposes that, together with the detection of intentionality, the detection of eye direction would be processed by a specific module. This module would first allow detecting eye-like stimuli and then act as a building block of shared attention mechanisms that allow us directing our attention synchronously onto the same object as an observed individual. Since this influential model was set, there have been a growth of studies on the cognitive processes and brain networks activated by the perception of others’ gaze.

The importance of gaze in social cognition

Others’ gaze direction primarily indicates their direction of attention and focus of interest in the surrounding space (Fig. 1). However, we infer much more from gaze than the direction of others’ attention. Gaze perception allows us inferring the intentions and desires of our congeners. For instance, as we naturally look at the objects of our environment which we prefer [8], other’s gaze direction can be automatically interpreted as a preference for the object of attention. This may explain why the perception of another agent’s gaze directed toward an object can influence the evaluation that we make of the looked-at object. Indeed, using a gaze-cuing attentional orienting paradigm, Bayliss, Paul, Cannon and Tipper [9] have recently shown that objects previously cued by another agent’s gaze direction are preferred to objects toward which no attention was manifested.

Moreover, there are strong and mutual influences of gaze and emotion. For example, target objects previously cued by the gaze of a happy face are preferred in comparison with target objects cued by the gaze of a disgusted face [10]. By contrast, uncued or not looked-at objects are subsequently liked equally whatever the expression of the face cue, thus emphasising the role of gaze as a vector of this affective transfer. Reciprocally, gaze direction can modify the meaning and social pertinence of expressed emotions. Namely, the perceived intensity of emotional expressions depends on the concomitant gaze direction. For instance, smiling faces with direct gaze are rated as happier than smiling faces with averted gaze. The perceived intensity of anger is also greater for angry faces with—conversely—direct relative to averted gaze, while fearful faces are perceived as more fearful with averted rather than direct gaze [11—13]. In agreement with these behavioural data, several studies have recently shown that the neural substrates of facial emotion processing are partly dependent on gaze direction [14—16].

Gaze direction can also influence our categorisation and judgment of other people. For instance, speeding up as well as slowing down of gender judgments under direct relative to averted gaze have both been observed under different task parameters [13,17,18]. Macrae’s group has also reported that faces shifting their gaze from the periphery toward the participant were liked better than faces shifting their gaze in the opposite direction [19,20]. Those faces were also judged more attractive, at least for female faces judged by male observers.

Thus, the perception of gaze direction can lead to elaborated social cognition processes and others’ gaze appears as a complex social signal, which is decoded by taking into account other aspects of the face as well as the social context. This raises the question of the neurocognitive processes subtending gaze perception. In order to start uncovering these processes, experiments have focused on the perception of gaze in neutral faces or that of isolated eyes. Furthermore, following the emphasis on shared attention mechanisms in Baron-Cohen’s [5] mind-reading model, these studies focused first on the processes linked to averted gaze perception.
Facing the gaze of others

Figure 1  Gaze is an essential social cue. (a) From four years of age, when a child is asked which sweet ‘Charly’ (the central smiley) prefers, he points to the ‘‘Twix’’. Autistic children are less likely to do so [7]. (b) Example of an attractive woman (Marilyn Monroe) looking at the reader (c) Example of a target that is invalidly cued by the gaze direction of a central face. Such situation induces a decrease in the speed of target detection as compared to the situation where the target is validly cued by gaze direction. (d) An object cued by the gaze direction of a disgusted face will be liked less than an object cued by the gaze of a happy face [10].

The neurocognitive processes associated with the perception of averted gaze

The perception of averted eyes, that is the perception of a gaze directed at the surrounding environment, is well known to induce an automatic shift of the observer’s spatial attention in the seen gaze direction. This, now classical, result has been obtained in Posner-like attention orienting paradigms [21] where the gaze is used as a central attentional cue. In such paradigms, a face is first presented centrally with direct or masked gaze. It is followed by the same face with the eyes looking either to the left or to the right. Then, after a variable time interval, a target is presented to the left or right of the face, that is, in the gazed-at or validly cued side or in the not looked-at or invalidly cued side (Fig. 1c). The subject’s task is usually either to detect, or discriminate, or categorise the target. Several studies have shown that validly cued targets are processed faster than invalidly cued ones [22—25]. This cueing effect has been reported for a wide range of stimulus onset asynchrony (SOA) between the averted gaze cue and the target, ranging from 100 ms to 700 ms. It can be observed even if the gaze looks to the opposite side of the target in eighty percents of the trials and the subject has been informed of this bias [22]. This has been taken as evidence that seen gaze direction is a compelling cue to the direction of others’ attention, which triggers reflexive, mandatory shifts of the spatial attention of the observer.

Following this line of research, many studies on the cerebral substrates of the processing of gaze direction have focused on the brain responses associated with the perception of averted gaze or that of eye direction changes, using direct gaze as a control condition or starting position. The viewing of faces with averted gaze as compared to that of faces with direct gaze as well as the viewing of moving eyes relative to that of static direct gaze or no gaze activate the human Superior Temporal Sulcus (STS) [26—28]. This region seems to contain representations of different gaze directions [29]. It is also activated during selective attention to gaze direction relative to selective attention to face identity. By contrast, the latter activates more ventral regions of the visual pathway including the inferior occipital gyrus (IOG) and the fusiform gyrus, which have both been involved in the processing of the invariant aspects of faces [27,30]. Furthermore, STS activation has been shown to be modulated by the context in which the gaze shift occurs. Namely, gaze shifts toward the side opposite to a just appeared checkerboard versus toward the very side of the checkerboard modulated the hemodynamic response of the STS, primarily in the right hemisphere [31]. The STS is also activated by the viewing of mouth movement and body motion [26,32,33]. Thus, this region has been proposed to be more generally involved in the processing of biological motion, including the changeable aspects of the face such as gaze direction and facial expressions, and in social attention and social perception [30,33—37]. Averted relative to direct gaze also activates the intraparietal sulcus (IPS), which is involved in spatial attention processes [26,27]. Furthermore, in a positron emission tomography (PET) study, Calder et al. [85] have shown that the medial prefrontal cortex (MPF), known to be involved in theory-of-mind tasks, would be primarily involved when viewing averted rather than direct gaze, although it seems to be activated for the processing of both direct and averted gaze.

As for the timing of the brain responses to gaze direction, there have been only a few electroencephalography (EEG) and magnetoencephalography (MEG) studies on the percep-
tion of gaze direction. Like those with functional magnetic resonance imaging (fMRI), these studies mostly focused on the perception of eyes moving sideways from a central position or on that of averted relative to direct gaze. They mainly reported an influence of gaze direction on the latency of the N170 (in EEG) and M170 (in MEG) evoked by faces, with earlier responses to faces with averted than direct gaze [38–40]. In an EEG version of their 1998’s fMRI study, Puce et al. [38] also reported greater N170 to frontal faces turning their eyes away from a central position than to faces turning their gaze back into the central position. Similar modulations of the N170 were induced by the opening (relative to the closing up) of the mouth. These modulations may thus reflect the STS activations that were observed with fMRI by Puce et al. [26]. However, other studies using static faces found very little, if any, effect of gaze direction on the amplitude of the N170 [40,41]. Moreover, using the same protocol as Puce et al. [38] but with MEG, Watanabe et al. [42] reported a greater 1M response (equivalent to the M170) for the gaze shifting from the periphery toward the subject than for the gaze averting away. In a very similar protocol, Watanabe et al. [43] also reported a smaller 1M response for the eyes turning sideways than for static eyes with direct gaze or for the radial motion of concentric circles. These discrepancies may be related to the differential sensitivity of MEG and EEG signals to distinct brain sources. However, it also calls attention on the use of direct gaze as a baseline condition in the study of the brain responses to gaze: what about gaze contact and the processes that may be specifically triggered by the perception of direct gaze?

The cognitive processes associated with the perception of direct gaze

In many respects, direct gaze or eye contact seems to constitute a singular direction of gaze [4,44,45]. Studies in social psychology emphasised the functions of gaze contact as a synchronisation signal between individuals [46]. For instance, eye contact plays a role in the regulation of interindividual exchanges, particularly during conversations, where it allows people to express expectancies and social control. Moreover, gaze contact can have various meanings, ranging from the expression of intimacy to that of dominance or hierarchical relationships [47]. This variety of meanings has been acquired through evolution, yet it shows a great diversification only in humans where the variety of meaning of direct gaze is highly dependent on the social context and the cultural codes that guide gaze behaviour. The meaning of direct gaze must thus be decoded as a function of the context and this, of course, encompasses the facial context. However, in any case, gaze contact signals mutual attention: it indicates that the attention of another agent is directed at oneself rather than onto an external object of the environment. In developmental psychology, current data suggest that human infants have an innate preference for faces with direct gaze [48]. Such early sensitivity may be the basis for the development of social cognition since direct gaze appears as the most rudimentary form of social contact [49].

Thus, overall, gaze contact appears as a particularly salient social stimulus and a signal to which we are exquisitely sensitive [50]. As a preliminary to interindividual interactions, it may be a strong cue for the allocation of resources to the processing of the seen face. This raises the following possibilities:

- there exist asymmetric mechanisms for the detection of gaze contact over other gaze directions;
- the perception of gaze contact relative to averted gaze may trigger enhanced neural processing of the face due to its social significance.

These questions have recently started to be actively addressed in our group.

Following a preliminary study by von Grünau and Anston [51], we used a visual search task to investigate the asymmetries in the detection of direct and averted gaze [52]. The subjects’ task was either to detect a direct gaze target embedded among averted gaze distracters or, conversely, to detect an averted gaze target among direct gaze distracters (Fig. 2a). The stimuli were realistic eyes taken from the photographs of full and deviated faces, in order to test for the influence of head orientation on the detection of...
Facing the gaze of others 201

gaze direction. We found first that direct gaze targets presented among averted gaze distracters were detected faster and better than averted gaze targets among direct gaze distracters, but only when the head was deviated. This may be related to the greater saliency of direct gaze under deviated than frontal head view, as incongruence between head orientation and gaze direction emphasises the directional intent of direct gaze. This result is in agreement with that of Senju et al. [53] who further showed that the advantage for direct relative to averted gaze detection under deviated head view was absent in children with autism [54]. Moreover, Conty et al. [52] showed that direct gaze targets were always detected quickly and efficiently, with little influence of the head orientation under which the gaze was seen and the visual field in which the direct gaze target was presented. By contrast, the detection of averted gaze was strongly modulated by these parameters. These results suggest that gaze contact has precedence over contextual information such as head orientation and visual field, which may be related to its social significance and behavioural relevance.

Another aspect of direct gaze direction concerns the allocation of resources that it may induce for the processing of seen faces. In agreement with this idea, it has been shown that gaze contact can capture visuospatial attention, resulting in delayed orienting of spatial attention toward peripheral targets cued by direct rather than averted or closed eye gaze [55]. Moreover, several studies have shown that faces with direct gaze are memorized better than faces with averted gaze [18,56–58]. For example, we used faces seen under frontal and deviated head views with direct and averted gaze to test for the influence of gaze direction and head orientation on face memory [18] (Fig. 2b). The faces were first presented during an initial gender categorisation task. This encoding phase was followed by an old/new recognition task that used the same faces randomly intermingled with new faces under frontal or deviated head view and with direct or averted gaze. We showed that the faces were better recognized under deviated head view and that, under this view, they were better recognized with direct than averted gaze. Other studies have found an advantage for direct over averted gaze on the memory for frontal views of faces [56–58]. Furthermore, in Vuilleumier et al. [18], the interaction between head orientation and gaze direction was particularly marked for faces of the opposite gender to the observer, which emphasises the integrative nature of the processing of social information during face perception.

Thus, there are asymmetries in the processing of gaze contact versus other gaze directions. While averted gaze elicits processes related to the orientation of spatial attention and to shared attention, direct gaze is associated with preferential detection mechanisms and triggers processes related to the analysis of faces. As a consequence, it may be expected that the perception of gaze contact activates a distinctive brain network.

The influence of direct gaze on the brain responses to seen faces

In a first series of experiments, we investigated the neural correlates of the processing of direct gaze in the context of face perception. Our aim was to check if gaze contact can increase the perceptual responses to seen faces such as that observed in the fusiform gyrus with fMRI [59,60–62], or such as the N170 in EEG and M170/OT165 in MEG [63–66].

In an fMRI study where we presented frontal and deviated views of faces with direct and averted gaze, we have shown increased fusiform responses to faces with direct relative to averted gaze [67] (Fig. 3). These responses were observed independently of head orientation. Thus, they could not be driven simply by low-level image properties such as symmetry in the eye region, which holds only for direct gaze in full-face views. Rather, the fusiform gyrus regions are known to be involved in the perceptual analysis of faces relative to other visual objects [59–62] and to show increased activation during enhanced attention to faces [27,68–70]. Thus, these responses are in agreement with the greater encoding and/or deeper attention allocated to faces seen with direct gaze, which is essential for decoding the meaning of gaze contact and leads to better recognition of these faces [18,58]. Such results are also consistent with the evidence of attentional capture by gaze contact [55]. Moreover, the processing of direct gaze involved the amygdala [67,71] (Fig. 3). This structure is known to play a central role in emotion and stimulus salience processing as well as in the social evaluation of faces [72–76]. This result is consistent with older studies that reported reduction of EEG activity in the alpha (8–13 Hz) band, known to be inversely correlated with vigilance level, in response to direct relative to averted gaze, in face-to-face interaction [77]. It is in agreement with the arousing value and social significance of gaze contact and may underlie the advantage for direct relative to averted gaze detection [52,53] as well as the better memory and preference for faces with direct gaze [18,19,58].

What about the time course of these processes? In an EEG-MEG study, we adapted the George et al. [67] fMRI protocol in order to examine the modulation of the early evoked magnetic fields (ERFs) and electric potentials (ERPs) in response to static frontal and deviated views of faces with direct and averted gaze (George et al., unpublished data). As in
George et al. [67], we used a gender categorisation task, thus examining the automatic influence of gaze perception on face processing. We first found that the early visual P100 component was not modulated by gaze direction. This is consistent with the fact that faces with direct versus averted gaze differ only subtly in terms of their low-level physical properties, around just the eye region. Moreover, the M170 and the N170 peaked around 150 ms. Although their functional role is still a matter of intense debate [78,79], these early magnetic and electric components have been associated to the early perceptual analysis of faces as compared to that of other non-face objects. In agreement with the enhanced attention and/or deeper encoding devoted to faces with direct gaze, both the M170 and the N170 were enhanced in response to faces with direct relative to averted gaze. However, this effect was confined to the right hemisphere in EEG and it was observed only under deviated head view in MEG. A main effect of gaze, independent on head orientation, was observed only between 200 and 250 ms in EEG, over posterior temporal regions, and between 200 and 450 ms in MEG, over anterior temporal sensors. Thus, these results showed an early influence of gaze direction on the M170 and N170 responses to faces, but which indicated an early integration of head orientation and gaze direction cues that are both indicators to the direction of others’ attention. Moreover, the scalp distribution of the later, sustained, main effect of gaze observed in both MEG and EEG suggests that this latter effect may be associated with the fusiform responses coupled with amygdalar activities observed under direct relative to averted gaze conditions in the George et al. [67] fMRI study.

In conclusion, in agreement with behavioural data, these brain imaging studies show that in the context of face perception and categorisation, direct gaze perception is associated with enhanced processing of the seen faces, involving the fusiform gyrus and the amygdala as well as the N/M170 and later temporal activities. These results are consistent with the social significance of direct gaze as a preliminary to interindividual interactions and, hence, as a strong signal for the allocation of resources to the processing of the seen faces.

### Brain responses to eye contact in the context of gaze movement

In real life conditions, movement is an essential component of gaze. Moreover, the use of moving eyes may favour the observation of brain responses associated with the processing of the gaze per se, whereas the use of static images of full views of faces may emphasise the processes related to the integrated processing of gaze and other facial aspects. Several studies examined gaze perception using moving eye stimuli. However, as mentioned earlier, these studies mainly focused on the processes related to averted gaze perception and this may have hindered the observation of the processes triggered by gaze contact. For instance, in some of these studies, direct gaze served as a control starting point condition before the eyes moved sideways (averted motion condition) and then returned to central position (direct motion condition), which may have biased the data toward eliciting greater brain responses to averted than direct gaze motion [26,38]. In another experiment, the amount of ‘implied motion’ [80] was greater in averted than direct gaze conditions [27,2]. By contrast, in a recent study, Pelphrey et al. [81] compared eye movements either toward the viewer or away from him/her, but always starting from a determinate position and implying the same movement quantity. In this condition, they found that direct gaze motion evoked greater STS activity than averted gaze motion did. Furthermore, in an EEG study, Senju et al. [82] examined changes in eye direction using faces glancing downward as a common starting gaze condition and they showed an enhanced N200 for faces establishing gaze contact in typically developed children. This shows that increased brain responses to gaze motion leading to gaze contact rather than to gaze aversion may be observed under appropriate conditions. We further investigated this issue in a recent EEG experiment.

In this experiment, we used faces suddenly turning their gaze toward the subject or away from him/her, in order to investigate if, in the presence of a face, gaze movement per se would be sufficient to elicit early activities related to the differential processing of direct versus averted gaze [83]. Faces seen under frontal and deviated head views with direct and averted gaze were included. An intermediate position of gaze was created by a morphing procedure and served as starting position under all conditions. Thus, frontal or deviated faces with intermediate gaze position were presented for 600 to 800 ms, then immediately followed by the same face under the same head view, with its gaze now either averted by 30° (averted gaze movement condition) or looking directly at the subject (direct gaze movement condition [83]) (Fig. 4a). In order to better isolate the processes related to the processing of gaze per se, we used an explicit task with regard to the direction of the gaze movement: the participants had to report whether the eyes of the stimulus were directing toward him/her or away from him/her. We then computed the ERPs time-locked to the movement onset. Our main results first show that the responses to direct gaze movements were faster than those to averted gaze movements, in agreement with former studies showing that we are biased at detecting direct as compared to averted gaze [52,53]. More interestingly, at the electrophysiological level, gaze movement elicited a clear N170 component, in spite of the presence of the face during the baseline period. This N170 was markedly enhanced under the direct as compared to the averted gaze condition (Fig. 4b). Furthermore, although this effect of the direction of gaze motion was significantly more marked under deviated than frontal head views, it was significant under both head orientations. The N170 component also peaked later and lasted longer in response to direct than averted gaze movement. Keeping in mind that the face was present during baseline, these N170 effects may be related either to a re-encoding of the face as it turned its gaze toward the viewer or to the enhanced processing of biological motion in the case of the eye movements that led to direct gaze. These results further support the idea that direct gaze as compared to averted gaze represents a greater source of information to extract, mobilizing more resources in the early stage of face and/or motion processing.

Moreover, an additional effect of the direction of gaze movement was observed over centroparietal regions...
between 160 and 210 ms, which was of the same order of magnitude as the occipitotemporal effect. The examination of the global "direct minus averted gaze" ERP difference further indicated that the differential activity elicited by the two gaze conditions culminated first over centroparietal regions around 185 ms, then extending over occipitotemporal regions where it culminated around 195 ms, overlapping the N170 response. Moreover, a local effect of Head Orientation significant under averted gaze only was observed in the central scalp region, which was not present over the occipitotemporal electrodes. Taken together, these results suggested that the centroparietal effect of gaze was not merely due to the spatial extension of temporal N170 activities and that multiple processes were involved in the early dissociation of direct and averted gaze conditions.

We thus turned to source analysis in order to identify the brain regions involved in these early differential responses, focusing on the 150—220 ms time-window. We performed a weighted minimum norm estimate (MNE) of the cortical sources of the ERP difference corresponding to direct minus averted gaze conditions with the Brainstorm Matlab Toolbox (http://neuroimage.usc.edu/brainstorm) [84]. This analysis revealed a structured network of differentially activated sources (Fig. 4c). First, two clusters of activities were observed in the dorsomedial prefrontal (MPF) regions. The first one was active from 150 to 160 ms until 210—220 ms and showed greater activity during averted relative to direct gaze. By contrast, the second one, which was significantly activated between 170 and 180 ms and 200—210 ms, showed greater activation for direct than averted gaze. Thus, these two clusters were functionally dissociated and corroborated the scalp data that showed clearly divergent activity for direct and averted gaze conditions between 160 and 210 ms over centroparietal electrodes. This source result is consistent with Calder et al. [85] PET finding of the medial prefrontal region involvement in the processing of both averted and direct gaze. Such MPF involvement underlines that both averted and direct gazes trigger processes of intention attribution associated with theory of mind, although of distinct nature. A third cluster of differentially activated sources was observed between 180 and 190 ms and 210—220 ms in the orbitofrontal (OFc) region and a fourth cluster was located in the region of the right STS between 190 and 200 ms and 200—210 ms. Both showed greater activity under direct than averted gaze conditions. This confirms the involvement of the STS in the processing of biological motion and social information conveyed by eye contact [81] and emphasises the early recruitment of such processes during direct gaze processing. Furthermore, the OFc region is known to be strongly interconnected with the amygdala [86] and to be involved in emotional processing as well as social intelligence [87—90] (for a recent review, see [91]). Its early differential activation to direct relative to averted gaze confirms the saliency and emotional significance of eye contact [67,71,16,20]. Altogether, these source localisation results support the involvement of the social brain network in the early dissociation between direct and averted gaze. This would subsume the efficient decoding of the meaning of

![Figure 4](image-url)

**Figure 4**  EEG experiment of Conty et al. [83]. (a) Example of a trial. (b) Scalp topography of the N170 represented on a back view of the head and N170 time course on one left (P7) and one right (P8) occipitotemporal electrodes for the four experimental conditions of direct (black lines) and averted gaze (gray lines) under frontal (solid lines) and deviated head views (dashed lines). The N170 was of greater amplitude, later latency and longer duration for direct than averted gaze. (c) Sources differentially activated for direct versus averted gaze, between 150 and 220 ms. Significantly activated sources are represented in white on frontal (i. and ii.), ventral (iii.) and lateral (iv.) views of a standard anatomical MRI template. Four clusters of sources were observed (i. to iv.). For each cluster, the bar-plot on the right shows the mean activity of the cluster under the direct (in black) and the averted gaze (in gray) conditions (expressed in z-score relative to the baseline period).
gaze contact, which is essential to the adaptation of one’s behaviour to this complex social signal.

Implications of this research

Others’ gaze direction appears as an essential social cue. Direct and averted gazes both trigger processes of mental state attribution and social attention, which are central to social cognition. However, these processes seem to be of quite distinct nature and the set of studies presented here confirms the existence of marked asymmetries in these processes that are associated with direct versus averted gaze perception. These asymmetries have been observed at the behavioural as well as the neural levels. In particular, gaze contact triggers preferential detection processes and greater face memorisation and this is associated with greater neural responses to the faces seen with direct gaze.

Within the network of brain regions activated by direct and averted gaze, it is interesting to note that some regions such as the STS and the MPF yield selective responses to both these gaze directions. This may be related to the role of these regions in the processes that the perception of both direct and averted gazes activates (such as biological motion processing and social attention for the STS and mental state attribution for the MPF). On the other hand, some regions, such as the IPS and the amygdala, seem to be specifically involved in the processing of either averted or direct gaze, respectively, in agreement with the distinctive primary meaning of these two classes of gaze directions.

Another dimension along which direct and averted gaze processing seem to vary importantly is related to the influence of head orientation. Gaze direction and head orientation both constitutes cues to the direction of others’ attention. Some models have proposed that gaze direction would be prominent over head orientation as a cue to one’s direction of attention [92]. Such view comes in particular from the recording of neurones selectively sensitive to gaze direction in the STS of macaque monkeys [93]. Some of these neurones are tuned to averted gaze while others are tuned to direct gaze and this selectivity to eye direction can be observed independently of head orientation. Moreover, if the eyes are masked, the neurones retain their selectivity to the direction of others’ attention as they fire for the head orientation corresponding to their preferred gaze direction (that is, frontal face for the neurones responding to direct gaze; deviated head for those activated by averted gaze). This has led Perrett et al. [92] to propose a model of the detection of the direction of others’ attention where eye direction is a prominent cue that can override the signal conveyed by head orientation which, in turn, can inhibit the cues from body orientation. Such model has been put into question by studies that showed mutual and similar influence of head and gaze in a task where the subject had to discriminate either the head orientation or the gaze direction [94]. However, interestingly, this latter study did not include direct gaze among the tested conditions. Our data may help reconcile these two opposite models of the integration of head cues during gaze processing. Indeed, in the light of the series of experiments run in our group, it may be proposed that the processing of averted gaze and that of head orientation always interact. This has been observed during gaze detection [52], but also during moving gaze discrimination where an effect of head orientation was observed in some scalp regions for averted gaze only [83]. By contrast, it seems that the influence of head orientation can be at least partly inhibited during direct gaze processing. This inhibitory process appears to take place particularly when gaze can be processed in isolation from the face. This was the case in Conty et al. [52] where eye-only stimuli were used, as well as in Conty et al. [83] EEG experiment where eye movement was dissociated from face presentation and the subject’s had explicitly to concentrate on gaze direction. On the other hand, the integration of head orientation cues during direct gaze processing may occur to greater extent when the task encourages the subjects to process the whole face (such as in gender discrimination and face recognition task; see also [95]). In conclusion, it is possible that the inhibition of head orientation postulated by Perrett et al. [96] would take place only during gaze contact processing. In agreement with this idea, Perrett and Emery [97] proposed the existence of two distinct modules involved in the detection of the direction of others’ attention, the first one dealing with mutual attention and mainly concerned with gaze contact processing, and the second one dealing with other directions of attention. This model is consistent with the dissociations between direct and averted gaze that we have observed as well as with a recent brain imaging study that has provided evidence for supramodal brain responses to signals conveying communicative intention toward the self [98].

Conclusion

Others’ gaze direction appears as an essential social cue (see also [99] for a recent review). Direct and averted gazes both trigger processes related to mind-reading and social cognition but of quite distinct nature. Thus, gaze perception activates a network of brain regions that show differentially selective responses to direct and averted eyes. While cognitive neuroscience studies have first focused on averted gaze, there is a growing amount of work underlining the saliency of gaze contact and our exquisite sensitivity to this singular gaze direction. These studies shed light on the wealth of processes associated with the perception of eye contact, encompassing preferential detection processes as well as increased memory and preference for faces seen with direct gaze, particularly under deviated head view. In agreement with these psychological data, direct gaze perception is associated with greater fusiform (in fMRI), N170 (in EEG) and M170 (in MEG) responses to the seen faces. It also triggers the early recruitment of the social brain network, within the first 200 ms following gaze movement. Future studies at the crossroad of social psychology and cognitive neuroscience will allow characterizing further the processes involved in the social perception of faces and the role of gaze contact in interpersonal interactions.

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Facing the gaze of others

References


