
Decoding Social Signals in the Infant Brain: A Look at Eye Gaze Perception.

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1. Introduction

An important social signal encoded in faces is eye gaze. The detection and monitoring of eye gaze direction is essential for effective social learning and communication among humans (Bloom, 2000; Csibra & Gergely, 2006). Eye gaze provides information about the target of another person’s attention and expression, and it also conveys information about communicative intentions and future behavior (Baron-Cohen, 1995). It has been argued that an early sensitivity to eye gaze serves as a major foundation for later development of social skills (Baron-Cohen, 1995; Csibra & Gergely, 2006; Hood, Willen, & Driver, 1998).

Over the last decades, a number of neuropsychological and neuroimaging studies have contributed to the identification of specialized cortical brain areas involved in gaze processing in adults (for an overview, see Table 1). Despite the progress in understanding the sophisticated gaze reading capacities and their neural basis in adults, the more basic question about the development and precursors of these adult abilities has been virtually unaddressed. In order to answer this question it is of particular importance to look at the earliest stage of postnatal development, i.e. infancy. Therefore, the goal of this chapter is to review and integrate the accumulating behavioral and neuroimaging work on the early emergence of the eye gaze processing system during infancy.

Before we turn to a review of the empirical work, it seems worthwhile to situate this work in the broader context of developmental theories of eye gaze perception. Let us therefore briefly consider theoretical accounts that have been put forward. Theories in this area differ with respect to (a) the degree to which gaze processing depends on experience and (b) the extent to which gaze processing is considered to be independent from other aspects of face processing. One influential theory proposed by Baron-Cohen (1994) stipulates that due to the adaptive importance of detecting eye gaze early in life, there is an innate module within the brain, the so-called Eye Direction Detector (EDD), which is specifically devoted to processing eye gaze. Furthermore, according to this account, the “eyes looking at me” simply
pop-out from a visual scene, which implies that this pop-out effect is independent from the face context. In contrast to this nativist and modular framework, other accounts argue that although there might be initial perceptual biases which guide infants’ behavior to eye gaze, these biases may be linked to more general mechanisms for detecting faces (Farroni et al. 2005; Johnson, 2005; for a detailed discussion see, Farroni, Menon, & Johnson, 2006) and/or communicative partners (Gliga & Csibra, in press). These accounts further acknowledge that experience plays an important role in the creation of the gaze perception system (Farroni et al., 2006; Vecera & Johnson, 1995). This latter theoretical standpoint, which puts forward that there are initial biases present in newborns that interact with experiential factors shaping the emergence of the gaze processing system during infancy, will be supported by the bulk of the empirical evidence presented in this chapter.

The structure of the chapter is as follows. First, we will discuss behavioral data drawn from three areas that we consider most relevant for the discussion of eye gaze perception in infancy: (1) eye contact detection, (2) gaze following, and (3) joint attention. This section will be followed by a thorough review of findings illuminating the neural basis of eye gaze perception in infancy. This represents the main focus of the chapter and it will build and directly follow up on the behavioral phenomena outlined earlier. The data that will be presented in this section are based on findings obtained by using electroencephalography (EEG)/event-related potential (ERP) methods, which are the neuroimaging methods most commonly used with infants. Note, however, that the fact that most of the neuroimaging work with adults relies on functional magnetic resonance imaging (fMRI) and that such data are missing with infants, partly limits the conclusions that can be drawn in terms of developmental comparisons between infants and adults especially as far as brain structures are concerned. In closing, we will integrate behavioral and neural findings and look ahead to make suggestions for future work.

2. Infants’ Behavior: Eye contact detection, gaze following, and joint attention
One critical aspect of gaze perception is the detection of eye contact, which enables mutual gaze with another person. Eye contact is considered to be the most powerful mode of establishing a communicative link between humans (Kampe, Frith, & Frith, 2003; Kleinke, 1986). Sensitivity to eye contact is evident early in human ontogeny, and is believed to provide a vital foundation for social cognitive development (Baron-Cohen, 1995). From birth, infants have a bias to orient toward face-like stimuli (see Johnson, 2005) and prefer to look at faces with their eyes open (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000). The most compelling evidence that human infants are born prepared to detect socially relevant information comes from work showing preferential attention in newborns to faces with direct gaze. In one study (Farroni, Csibra, Simion, & Johnson, 2002), human infants’ eye movements were recorded while a pair of face stimuli was presented: one face directed eye gaze at the newborns and the other directed eye gaze away (see Figure 1A). The analysis of newborns’ eye movements revealed that fixation times were significantly longer for the faces with direct gaze when compared to faces with averted gaze. Furthermore, the number of orienting looks to the direct gaze was also higher than for averted gaze.

Hitherto, the finding of an eye contact preference in newborns has been replicated using a different set of photographic face stimuli (Farroni et al., 2006) and was also obtained when schematic faces were used (Farroni, Pividori, Simion, Massaccesi, & Johnson, 2004). However, the preference for direct gaze in newborns is present only within the context of an upright face and a straight head (Farroni et al., 2006). In other words, when direct and averted gaze faces are presented upside down or with the head turned to the side (see Figure 1B and C), then newborns fail to show a preference for eye contact. The finding that newborns do not show a preference when inverted faces are used rules out lower-level explanations of the original result (Farroni et al., 2002) such as a preference for symmetry (direct gaze) over asymmetry (averted gaze). Furthermore, the strong tendency of newborns to orient to faces with direct gaze only under conditions of an upright and straight-head face is consistent with
the view that relatively simple perceptual biases and configuration-sensitive mechanisms may be driving this early eye contact preference (Farroni et al., 2002). This view was advanced by Farroni, Mansfield, Lai, and Johnson (2003), who tried to integrate the evidence of infants’ perception of eye gaze with the earlier “two-process”-theory of face recognition. More specifically, Johnson and Morton (1991) hypothesized that newborns have a primitive mechanism (termed Conspec for context-specific) that biases them to orient toward the basic configuration of faces such as high-contrast areas corresponding to the eyes and mouth.

Farroni and colleagues (Farroni et al., 2002; 2003) suggested that the same mechanism could also determine the preference of newborns for direct gaze. This is because a mechanism that relies on darker elements on a lighter background might help the infant to find a face in the distance or the periphery but could also support eye-contact detection at close proximity (for a discussion, see Farroni et al., 2005). Such a basic mechanism may bias the input to the developing brain, ensuring that during later postnatal development infants develop expertise for faces, including eye gaze processing. However, this idea remains to be tested.

Another important aspect of eye gaze processing is that averted gaze triggers a reflexive shift of an observer’s visual attention (e.g., Driver et al., 1999). Numerous studies have investigated the effects that perceived gaze direction has on spatial attention in adults (e.g., Friesen & Kingstone, 1998; Langton, Watt, & Bruce, 2000). The robust finding in these studies is that observers are faster to detect a target stimulus occurring in the peripheral visual field if it is preceded by a face looking to the same direction than when the preceding face is looking to the opposite direction. Newborns have also been found to be faster in making saccades to peripheral targets cued by the direction of eye movements of a schematic face, suggesting a rudimentary form of gaze following (Farroni, Pividori et al., 2004). By the age of 3 months, human infants are more likely to orient towards a target stimulus if it is preceded by a perceived gaze shift in the same direction when photographic images of a face are used (Hood et al., 1998).
Four-month-old infants were tested using a cueing paradigm adapted from Hood et al. (1998) to further examine the visual properties of the eyes that enable infants to follow the direction of someone’s gaze (Farroni et al., 2003). This series of experiments revealed that infants, in contrast to adults, need to see eye-movements to show a gaze-following effect, but motion alone is insufficient to shift infants’ attention as gaze shifts in an inverted face does not elicit gaze-following (this finding has been replicated with newborns, see, Farroni, Pividori et al., 2004). Moreover, to find this effect in infants, the face has to be removed before the target object is presented, a finding that may be linked to young infants’ difficulty in disengaging from attractive stimuli (Johnson & Morton, 1991), and the gaze cueing has to be preceded by a period of mutual gaze in order for it to be effective. The latter finding supports what was said earlier about the important role that eye contact plays in establishing social communication between humans. In summary, the critical features for eye gaze cueing in young infants are (1) an upright face, (2) a brief preceding period of eye contact, and (3) lateral motion of the eyes.

The youngest age at which infants have been found to follow the gaze of live partners is between 2 and 3 months (D'Entremont, Hains, & Muir, 1997; Scaife & Bruner, 1975). Again, the gaze following response requires special triggering conditions, including constant infant-directed speech and target objects that are very close to the presenter’s face. By about 6 months, infants follow gaze to more distant targets (Butterworth & Itakura, 2000; Butterworth & Jarrett, 1991), and gaze following responses to a target become reliable between 7 and 9 months of age (Flom & Pick, 2005; Woodward, 2003). However, the precision of 9-month-olds' responses is still fragile when several potential targets are available (Flom, Deak, Phill, & Pick, 2004). This is because infants around this age usually direct their gaze to the first object on the correct side (Morales, Mundy, & Rojas, 1998). Furthermore, 9-month-old infants follow the head turn of someone whose eyes are closed, whereas only a month later they do not (Brooks & Meltzoff, 2005). Only by around 12 months do infants encode the
psychological relationship between a person and the target of her gaze (Woodward, 2003).
However, until the age of 14 months, infants follow blindfolded people's head turns (Brooks & Meltzoff, 2002), whereas after this age, infants start to take into account whether the other has visual access to the target object (Caron, Keil, Dayton, & Butler, 2002; Dunphy-Lelii & Wellman, 2004) and to correctly integrate information from head and eye direction (Caron, Butler, & Brooks, 2002).

The development and improvement of the described gaze following capacities in infants might be governed by different age-specific mechanisms (for a comprehensive theory, see Butterworth, 1991), and it is generally thought that this development serves the function of coordinating visual attention with other humans and thereby achieving joint attention with them (Tomasello, 1999). More specifically, it has been hypothesized to serve various functions, including (a) instrumental learning/obtaining rewards by catching sight of something interesting (Moore & Corkum, 1994), (b) identifying others’ attentional or perceptual states (Baron-Cohen, 1991), and (c) finding out what the other person is communicating about (Csibra, submitted).

To summarize, newborns enter the world with initial perceptual and attentional biases that lead them to attend to eye gaze information encoded in a person’s face. As outlined above, these biases seem to rely on certain triggering conditions and are specifically tuned to upright faces. With development, infants’ behavior becomes more flexible and accurate not only in discerning a person’s gaze direction but also in linking another person’s gaze and visual access to particular objects and events in the environment.

Although behavioral data remains an important source of information for developmental scientists, the successful application of neuroimaging methods to developmental populations has shed light on neural mechanisms that underlie infants’ ability to read the language of the eyes. Therefore, in the next section we will focus on the neural basis of eye gaze perception in infancy and try to integrate neural level findings with the
behavioral data presented in this section.

3. Neural basis of eye gaze perception in the infant brain

3. 1. Gaze direction perception

The question we are trying to address in this section is, what are the neural underpinnings of infants’ behaviorally expressed preference for mutual gaze and the capacity to follow gaze? As already pointed out in the introduction, our review will focus on findings obtained by using EEG/ERP methods. Farroni and colleagues (2002) measured 4-month-old infants’ ERPs to examine neural processing of faces when accompanied with direct or averted gaze. In this study, an occipito-temporal ERP component (N170/N290) known to be sensitive to faces in adults (Bentin, Allison, Puce, Perez, & McCarthy, 1996) and infants (de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003; Halit, Csibra, Volein, & Johnson, 2004) was larger in amplitude in response to direct gaze than to averted gaze. This indicates that the presence of direct gaze enhances the neural processes in the infant brain that are associated with the earliest steps of face encoding (Farroni et al., 2002).

These findings have been replicated and extended by Farroni and colleagues, who found that in 4-month-old infants, an enhanced cortical processing of direct gaze is obtained even when the head is averted but direct mutual gaze is maintained (Farroni, Johnson, & Csibra, 2004). However, enhanced neural processing to faces with direct gaze is only found when eyes are presented in the context of an upright face, since in a second experiment, no differential cortical processing was observed when direct and averted gaze faces were presented upside-down. It is interesting to note that this series of ERP experiments in 4-month-olds (Farroni et al., 2002; Farroni, Johnson et al., 2004) follow the same logic (upright versus inverted face; straight versus oriented head) using the same stimuli (see, Figure 1) as the behavioral work with newborns and are therefore an important extension of this work. This enables us to assess the developmental trajectory by comparing the behavioral data in newborns with the ERP data in 4-month-olds (see, Table 1). Newborns show a strong
preference for direct gaze faces and this preference requires the context of an upright human face (Farroni et al., 2006). Similarly, 4-month-olds show an enhanced processing of direct gaze upright but not inverted faces (Farroni et al., 2002; Farroni, Johnson et al., 2004). However, newborns do not exhibit a behavioral preference for direct gaze faces when the head is averted, whereas direct gaze elicits an enhanced cortical response for both straight and averted head angles (see, Table 1). This suggests that with development and experience young infants’ gaze perception abilities become more flexible in the sense that they learn to extract information about mutual gaze independent of the head angle. A caveat to this conclusion is that different testing techniques were used with the different age groups. Thus, it remains possible that the differences observed are due to the measurement techniques rather than to the age groups tested.

Although the ERP studies have provided some insights into how infants process faces with direct and averted gaze, scalp-recorded ERPs do not yield direct information about the underlying brain sources. Johnson et al. (2005) applied independent component analysis (ICA) to a previously published data set (Farroni et al., 2002) in order to uncover the brain sources sensitive to eye gaze. ICA is a statistical source separation technique (Makeig, Debener, Onton, & Delorme, 2004), which has been successfully employed to localize sources of infant electrophysiological recordings (Richards, 2004, 2005). Consistent with earlier ERP findings (Farroni et al., 2002), Johnson et al. (2005) identified brain sources in 4-month-old infants’ occipital and temporal areas discriminating between direct and averted gaze. Contrary to adults, who show specific activations associated with eye gaze perception in the superior temporal sulcus (STS) (Allison et al., 2000), in infants, cortical generators localized in the fusiform gyrus discriminated gaze direction best. Furthermore, while it has been shown that the amplitude of the N290 in infants is modulated by eye gaze (Farroni et al., 2002; Farroni, Johnson et al., 2004) and face orientation (de Haan et al., 2002; Halit et al., 2003), the amplitude of the adult N170 is only affected by face inversion but not by direction
of gaze (Grice et al., 2005; Taylor, Itier, Allison, & Edmonds, 2001). Taken together, these differences between infants and adults suggest that face and eye gaze share common patterns of cortical activation early in ontogeny which later partially dissociate and become more specialized.

In addition, ICA analysis revealed further sources that were sensitive to gaze direction, and a subsequent localization attempt estimated that these sources originated from the prefrontal cortex. Such an effect was not revealed in traditional ERP analyses, illustrating the power of statistical source separation methods (Makeig et al., 2004). These prefrontal sources are of particular interest because functional magnetic resonance imaging (fMRI) studies show that prefrontal brain structures are activated by the detection of direct gaze and/or communicative intent in adults (Kampe et al., 2003; Schilbach et al., 2006).

Another technique that can reveal brain activation missed by averaging methods is the analysis of high-frequency oscillations in the gamma band (20-100 Hz). Such oscillations are either time-locked to eliciting stimuli (evoked gamma activity) or can be detected as induced gamma activity consisting of oscillatory bursts whose latency jitters from trial to trial and whose temporal relationship with the stimulus onset is fairly loose. Hence, induced gamma activity is not revealed by classical averaging techniques and specific methods based on time-varying spectral analysis of single trials are required to detect it (Tallon-Baudry & Bertrand, 1999). Gamma oscillations are of special interest because they have been found to correlate with the BOLD response used in fMRI (Foucher, Otzenberger, & Gounot 2003; Fiebach, Gruber, & Supp, 2005), and it is thought that activity in the gamma range serves as a mechanism to integrate activity from various, highly specialized brain areas (Gruber, Trujillo, Giabbioconi, Vales-Sosa & Mueller, 2006; Tallon-Baudry & Bertrand, 1999; Rodriguez et al., 1999).

Gamma oscillatory activity in infants has primarily been studied only in the context of object processing (Csibra, Davis, Spratling, & Johnson, 2000; Kaufman, Csibra, & Johnson,
2003, 2005). However, in a recent study (Grossmann, Johnson, Farroni, & Csibra, 2007), we examined gamma oscillations and its relationship to eye gaze perception in 4-month-old infants. This study was based on a time-frequency analysis performed on two previously published EEG data sets taken from Farroni et al.’s 2002 and Farroni, Johnson et al.’s 2004 ERP studies. Infants were presented with upright images of female faces directing their gaze toward them or to the side (see, Figure 1A). We predicted a burst of gamma oscillation over prefrontal sites to direct gaze if gamma oscillations are indeed related to detecting eye contact/communicative intent as suggested by adult fMRI work (Kampe et al., 2003; Schilbach et al., 2006). Averted gaze also serves an important function during communication by directing the perceiver’s attention to certain locations or objects, and behavioral measures have shown that infants are sensitive to this aspect of eye gaze (Farroni et al., 2003; Hood et al., 1998). The right intraparietal sulcus (IPS) and right STS, which have been identified as sensitive to averted gaze in the adult brain (Hoffman & Haxby, 2000), are potential candidates generating effects observable in infants. Therefore, we hypothesized that some activity over right posterior regions would be associated with the perception of averted gaze. In addition, another group of 4-month-old infants were presented with the same face stimuli upside-down (see, Figure 1B), which is thought to disrupt configural face processing (Rodriguez et al., 1999; Turati, Sangioli, Ruel, & de Schonen, 2004) and infants’ preference for mutual gaze (Farroni et al., 2006). Thus, we predicted that inverted faces would not induce activity in the gamma band that differs as a function of eye gaze.

The data revealed that evoked and induced gamma oscillations varied as a function of gaze direction in the context of an upright face, which extends previous ERP and source localization results (Farroni et al., 2002; Farroni, Johnson et al., 2004; Johnson et al., 2005). In support of our hypotheses, specific effects with distinct spatial and temporal characteristics were observed depending upon whether gaze was directed at or directed away from the infant. Direct gaze compared to averted gaze evoked early (100 ms) increased gamma activity (20-40
Hz) at occipital channels. Short-latency phase-locked oscillatory evoked gamma responses have been described in the visual modality in response to brief static stimuli in infant and adult EEG (Csibra et al., 2000; Tallon-Baudry & Betrand, 1999). In adults, it has been shown that evoked gamma activity is significantly larger for items that match memory representations (Herrmann, Lenz, Junge, Busch, & Maess, 2003; Herrmann, Munk, & Engel, 2004). It is possible that for infants a face with direct gaze represents a more prototypical ('better') face (Farroni, Massaccesi, Menon, & Johnson, 2007), which is closer to what is represented in memory than a face with averted gaze, and therefore elicits an enhanced evoked oscillatory response. This interpretation is supported by, and might be linked to, findings showing an enhanced neural encoding (Farroni et al., 2002) and better recognition of upright faces with direct gaze in infants (Farroni et al., 2007).

As predicted, direct gaze also elicited a late (300 ms) induced gamma burst over right prefrontal channels. In a previous analysis based on ICA, cortical sources sensitive to gaze direction had been identified in prefrontal regions (Johnson et al., 2005), which is consistent with the described finding. Directing eye gaze at someone (i.e., making eye contact) serves as an important ostensive signal in face-to-face interactions that helps establishing a communicative link between two people. It has been argued that successful communication between two people crucially depends on the ability to detect the intention to communicate conveyed by signals directed at the self such as making eye contact (Kampe et al., 2003). On a neural level, the dorsal part of the right dorsal medial prefrontal cortex (MPFC) has been found to be consistently activated when gaze is directed at, but not when gaze is averted away from, the self (Kampe et al., 2003; Schilbach et al., 2006). It is important to note that gamma oscillations measured with EEG have been found to correlate with the BOLD response used in fMRI (Fiebach et al., 2006; Foucher et al., 2003). It is thus possible that eye contact detection in 4-month-old infants recruits very similar brain mechanisms as in adults. Alternatively, it has been found that emotional processing, regardless of valence, enhanced
gamma band power at right frontal electrodes in adults (Müller, Keil, Gruber, & Elbert, 1999), and infants might have perceived the faces with direct gaze as more emotionally engaging which resulted in similar gamma responses as in adults.

Averted gaze also serves an important function during social communication by directing the perceiver’s attention to certain locations or objects, and there is behavioral evidence that 4-month-olds are sensitive to this aspect of eye gaze (Farroni et al., 2003; Hood et al., 1998). The right IPS and right STS have been identified as sensitive to averted gaze in the adult human brain (Haxby, Hoffman, & Gobbini, 2000; Hofman & Haxby, 1999). It has been argued that activity in the IPS is specifically recruited when perceived eye gaze direction elicits a shift in spatial attention, whereas STS is more generally associated with eye and mouth movements (Haxby et al., 2000). Our finding of a late (300 ms) induced gamma burst in response to averted gaze over right occipito-temporal-parietal regions might reflect similar but perhaps more diffuse brain activations in infants.

In another study (Grossmann, Johnson, Farroni, & Csibra, unpublished), we further examined how head orientation would influence the infants’ brain responses to eye gaze direction cues observed in the gamma band. This study was based on a time-frequency analysis performed on a previously published EEG data set taken from Experiment 1 of Farroni et al.’s 2004 ERP study. Infants were presented with upright images of female faces orienting their head away from the infant but either directing their gaze towards them or away from them (see Figure 1C). Corresponding with the findings reported for straight head angle faces, direct gaze compared to averted gaze elicited early (100 ms) increased gamma activity (20-40 Hz) at occipital channels. However, contrary to the previous findings (Grossmann et al., 2007), no induced gamma burst was observed over prefrontal channels to direct gaze when the head was averted. This suggests that although infants at the age of 4 months can discriminate between direct and averted gaze in the context of averted heads as indicated by the increased evoked occipital gamma activity to direct gaze, in this context, they do not yet
recruit brain processes associated with detecting eye contact as a communicative signal. Hence, it follows that by 4 months a frontal face is required to elicit activity in prefrontal brain structures involved in social communication. This finding stands in contrast to fMRI work showing that adults show specific activity in the prefrontal cortex in response to direct gaze even when the head is averted from the perceiver (Kampe et al., 2003) and therefore suggests that development must occur after 4 months which enables the human brain to detect mutual gaze regardless of head orientation.

Furthermore, as in the previous study using faces with a frontal orientation (Grossmann et al., 2007), we observed a late (300 ms) induced gamma burst over right temporo-parietal regions, but whereas when frontal faces were used this burst was evoked by averted gaze, for oriented faces this activity occurred in response to direct gaze. These seemingly contradictory findings need explanation. Our suggestion is that the gamma activity observed over right temporo-parietal channels is associated with neural computations integrating eye gaze direction information in relation to head angle. When the results are revisited from this perspective, it appears that this gamma burst is observed when eye direction is different/incongruent from the head direction (i.e., averted gaze in a frontal face and direct gaze in an oriented face). This view is in accordance with adult fMRI data showing increased activity in the right STS to averted gaze in frontal face (Hoffman & Haxby, 1999) and to direct gaze in averted face (Pelphrey, Viola, & McCarthy, 2004).

More generally, the lateralization of the induced gamma band effects to gaze direction cues to the right hemisphere observed in these studies might be due to the fact that (1) the brain mechanisms underlying eye gaze perception show a high degree of specialization early in ontogeny, recruiting very similar brain areas in the right hemisphere as in adults, (2) the right hemisphere dominance for the observed effects is simply due to the higher metabolic rate (Chiron et al., 1997) and earlier maturation of the right hemisphere observed during infancy (Thatcher, Walker, & Guidice, 1987), and/or (3) eye gaze perception triggers
emotional processes in the infant, which have been shown to result in a lateralization of the gamma band effects to the right in adults (Müller et al., 1999).

The finding that inverted faces did not elicit gamma band responses that differed between direct and averted gaze is in line with, and adds further developmental evidence to, the notion that face inversion disrupts face processing (Rodriguez et al., 1999; Turati et al., 2004). This indicates that relatively early in development cortical structures involved in face processing are already somewhat specialized to extract information about gaze direction from upright faces. It further shows that the gamma band effects observed in response to direct and averted gaze are not simply driven by ‘lower level’ perceptual parameters (e.g. symmetry [direct gaze] and asymmetry [averted gaze]) because then they should have occurred in the inverted condition as well. It is also important to note that these gamma band findings in infants show a high degree of correspondence in terms of timing and frequency content with previous findings in adults (Tallon-Baudry & Bertrand, 1999). This suggests continuity throughout development, and further underlines the functional importance of gamma band oscillations also for social perception.

To summarize, the ERP, source localization, and gamma band findings reviewed here provide important insights into the neurodevelopmental origins of eye gaze direction perception in infancy (see, Table 1). The systematic investigation of neural responses to direct and averted gaze in the context of upright versus inverted and frontal versus oriented faces reveal that (1) neural mechanisms are tuned to extract gaze information from upright faces, (2) with development young infants’ gaze perception abilities become more flexible in the sense that they learn to extract information about mutual gaze independent of the head angle, but (3) only frontal faces with direct gaze recruit brain processes which may reflect the detection of eye contact as a communicative signal.

3. 2. Neural basis of referential gaze perception and joint attention
As already alluded to in previous sections of this chapter, one important communicative function of eye gaze is to direct attention to certain locations, events, and objects. Understanding the relations between eye gaze and target objects is particularly important for aspects of development such as word learning. Comprehending that another’s gaze direction refers to a specific object allows the child to associate the object with a name or emotional expression (Baldwin & Moses, 1996). Adults’ gaze has been found to facilitate object processing at a neural level in infants as young as 4 months (Reid, Striano, Kaufman, & Johnson, 2004). In this ERP study, objects that were previously cued by eye gaze elicited a diminished positive slow wave observed between 700 and 1000 ms over right fronto-temporal channels. A diminished positive slow wave is thought to indicate deeper memory encoding (Nelson & Collins, 1991). This suggests that eye gaze as a social cue facilitates brain processes involved in memory encoding that might assist infants’ learning.

In another ERP study, 9-month-old infants and adults watched a face whose gaze shifted either toward (object-congruent) or away from (object-incongruent) the location of a previously presented object (Senju, Johnson, & Csibra, 2006). This paradigm was based on that used in an earlier fMRI study (Pelphrey, Singerman, Allison, & McCarthy, 2003) and was designed to reveal the neural basis of “referential” gaze perception. When the ERPs elicited by object-incongruent gaze shifts were compared to the object-congruent gaze shifts, an enhanced negativity around 300 ms over occipito-temporal electrodes was observed in both infants and adults. This suggests that infants encode referential information of gaze using similar neural mechanisms as those used by adults. However, only infants showed a fronto-central negative component that was larger in amplitude for object-congruent gaze shifts. It is thus possible that in the less specialized infant brain, the referential information of gaze is encoded in broader cortical circuits than in the more specialized adult brain. We will return to this interesting finding on referential gaze in the following paragraphs in which the neural
One of the major developmental changes in infants’ engagement with others is the transition from participating in dyadic (face-to-face) interactions to developing a capacity to engage in triadic (infant-other-object) joint attention exchanges. Besides attending to an external object or event herself, the ability to jointly attend with another person requires the infant to monitor (a) the other person’s attention in relation to the self and (b) the other person’s attention toward the same object or event. The establishment of joint attention and the monitoring of joint attention interchanges in preverbal infants heavily rely on eye gaze cues. Triadic relations between two minds and an object are thought to be uniquely human representations (Baron-Cohen, 1995; Tomasello, Carpenter, Call, Behne, & Moll, 2005), supporting shared attention and collaborative goals. The dorsal part of the medial prefrontal cortex has been identified as the neural substrate supporting these kinds of representations in the adult human brain (Frith & Frith, 2006; Saxe, 2006). It has been shown that already by 3 months of age, infants are able to behaviorally discriminate between dyadic and triadic joint attention interactions (Striano & Stahl, 2005). In this study, infants gazed and smiled more in the joint attention condition, in which an experimenter alternated visual attention between the infant and the object than when she simply looked at the object without engaging or addressing the infant. Despite this early sensitivity to triadic interactions, a more robust understanding of joint attention is not in place until 9 months of age (Tomasello et al., 2005).

Striano, Reid, and Hoehl (2006) used a novel interactive paradigm to examine the ERP correlates of joint attention in 9-month-old infants in which an adult interacted live with each infant in two contexts. In the joint attention context the adult looked at the infant and then at the computer screen displaying a novel object, whereas in the non-joint attention context the adult only looked at the novel object presented on the screen. Objects presented in the joint attention context compared to objects in the non-joint attention context were found to elicit a
greater negative component (Nc) peaking around 500 ms with a maximum over frontal and central channels. The Nc is generated in the prefrontal cortex and indicates the allocation of attention to a visual stimulus, with a greater amplitude indexing more allocation of attentional resources (Reynolds & Richards, 2005). Therefore, Striano, Reid et al. (2006) suggested that infants benefit from the joint attention interaction and thus devote more attentional resources to those objects presented in this context. Another interesting finding from this study is that the amplitude of the Nc in both contexts appeared to be substantially larger than in previous ERP studies (de Haan & Nelson, 1997; 1999). It is possible that rather than viewing the stimuli passively on the screen as in the previous work, the application of a novel interactive paradigm increased the social significance for the infant as reflected in a general increase in amplitude of the Nc.

It is worth noting that in Senju et al.’s (2006) study on referential gaze perception, which we discussed earlier, a very similar fronto-central negativity was observed as in Striano, Reid et al.’s (2006) live joint attention study. This is not surprising given the striking similarity between the two studies and the joint attentional nature of the situations presented to the infant in the two experiments. In Senju et al.’s study the fronto-central negativity was obtained in 9-month-olds who watched a person on the screen make eye contact and then look at an object, and in Striano, Reid et al.’s (2006) study, this brain response was obtained when a live experimenter established eye contact with the infant and then looked at an object on the screen. We therefore suggest that, as previously argued by Striano and colleagues, the joint attentional nature triggered mainly by eye gaze cues used in Senju et al.’s study can account for their finding of a fronto-central negativity to congruent gaze shifts.

In summary, there is evidence that joint triadic interaction with the infant indeed has an effect on brain structures, probably localized in the prefrontal cortex, that are associated with the allocation of attentional processing resources (Striano, Reid et al., 2006). This provides support for the view that social information has an impact and interacts with
attentional processes (Grossmann, Striano, & Friederici, 2005, 2007), which might point to an important mechanism of how social interaction influences information processing early in development. Based on behavioral findings, we stated that one of the major developmental changes in infants’ engagement with others is the transition from participating in dyadic (face-to-face) to triadic (infant-other-object) joint attention exchanges. This behaviorally evident transition has not been examined in the studies summarized here, since infants were only tested at ages at which they already engage successfully in triadic interactions. Thus, in order to elucidate the brain mechanisms underlying behavioral change, it seems worthwhile to also test younger infants.

4. Conclusions

Various behavioral and neuroimaging (ERP, source localization, gamma band analysis) methods have successfully been used to study different aspects of eye gaze processing in infants. The available evidence on the behavioral and neural processes related to eye gaze direction processing, gaze following/referential gaze and joint attention discussed in this chapter reveal insights into how the infant brain processes information about social gaze. Probably the most telling finding from all these studies is that the eyes provide a number of relevant social cues to which humans are sensitive from very early on in development. Moreover, the ability of the infant to decipher and interpret these various eye gaze cues in the face is associated with neural activity in a network of brain areas and cannot be assigned to a singular module or mechanism. In summary, infants show specific modulations of cortical responses associated with eye gaze perception, which differ partly from what is seen in adults. Nevertheless the findings reviewed also suggest that infants successfully discriminate between direct and averted gaze, and can make use of gaze cues when encoding objects in memory, following the gaze of another person, or jointly attending with another person to an object. This suggests relatively early functioning of the brain structures involved in perceiving
and acting on the eyes. However, this functioning may be broadly tuned, and less specialized, than that seen in adults.

The findings on eye gaze perception reviewed here can be seen as one aspect of social brain development and should therefore be integrated into a broader theory of the emergence of the social brain network during infancy (see, Grossmann & Johnson, 2007). Converging evidence indicates that even newborn humans are preferentially attentive to conspecifics, possibly due to sub-cortical routes for directing attention to social stimuli (Johnson, 2005). This preferential attention to conspecifics and their interactions will provide the appropriate input for developing cortical circuitry over the first few months. This input may ensure that a typical pattern of specialization into a cortical social brain network emerges (Johnson, 2005). According to this view, most parts of the social brain network including the areas involved in gaze processing can be activated in infants, though activation may also extend to other regions not activated under these circumstances in adults (Grossmann & Johnson, 2007). Further, the social brain regions activated may have broader functions (i.e., be less finely tuned) than in adults. Some of the evidence consistent with this view is that, compared to adults, (1) infants activate additional cortical processes when processing eye gaze (Senju et al., 2006) and (2) the cortical mechanisms in infants for detecting eye contact as a communicative signal are less finely tuned than in adults (Grossmann et al., 2007, unpublished). Furthermore, face and eye gaze perception have been shown to share common patterns of cortical activation early in ontogeny, which later partially dissociate and become more specialized (Farroni et al., 2002; Farroni, Johnson et al., 2004; Grice et al., 2005; Johnson et al., 2005; Taylor et al., 2001). These findings support the view that structures in the social brain network initially have more homogeneous response properties, with common processing of many aspects of faces, eyes, bodies and actions (Grossmann & Johnson, 2007). With experience, these structures may become more differentiated and specialized in their response properties, finally resulting in the specialized patterns of activation typically observed in adults. This view has implications
for atypical development in that some developmental disorders that involve disruption to the social brain network, such as autism, may be characterized in terms of failures or delays of the specialization of structures in the cortical social brain network (see Johnson et al., 2005, for further discussion).

As a part of the integration into a broader theoretical framework on how the social brain develops, it seems also important to understand how eye gaze processing interacts with other domains attributed to the social brain. For example, very little is currently known about how eye contact influences the processing of emotional expressions in the infant brain. It has been previously argued that direct gaze is likely involved in the communication of increased emotional intensity, regardless of the particular emotion being expressed (Kimble & Olszewski, 1980; Kleinke, 1986). Despite the intuitive appeal of the long-standing notion that direct gaze may facilitate emotional expression processing, recent brain and behavioral research with adults has shown that the way in which gaze direction influences emotion perception depends on the emotion in question (Adams & Kleck, 2003, 2005; Adams et al., 2003). For example, averted gaze enhanced the perception of fear faces whereas direct gaze enhanced the perception of angry faces (Adams & Kleck, 2005). The question of how eye gaze interacts with emotional expression has also been examined in young infants using ERP measures (Striano, Kopp, Grossmann, & Reid, 2006). In this study, 4-month-old infants were presented with neutral, happy, and angry facial expressions when accompanied with direct and averted gaze. The results show that neural processing of angry faces is enhanced in the context of direct gaze, whereas there is no effect of gaze on the processing of the other expressions. Although this neural sensitivity to the direction of angry gaze can be explained in different ways (for a discussion, see Grossmann & Johnson, 2007), it nevertheless is important to note that the neural processing of facial expression is influenced by the direction of eye gaze.
Whether or not this eye gaze interaction with emotional expression depends on experience has recently been investigated in newborns (Farroni, Menon, Rigato, & Johnson, 2007). When a fearful expression was compared to an happy one, newborns looked significantly longer at the happy face. This preference for the happy face was not obtained when gaze is averted (Menon, Farroni, Rigato, & Johnson, in preparation). One idea is that perception of facial expressions is acquired through experience and the perceptual dimensions relevant for different expressions are gradually discovered and used to differentiate perceptual inputs and associate them with different responses and consequences (Quinn & Johnson, 1997). It is possible that a happy face with direct gaze is preferred during the first few days of postnatal life because this facial expression is likely to be the most common face stimulus in the newborns’ experience with the visual world.

On a more general note, further progress in infant social cognitive neuroscience crucially depends upon advances on three levels: (1) the development of experimental paradigms that better approximate real life, (2) improvement in neuroimaging methods that suit infants, and (3) integration of theories of functional brain development with theories of social cognitive development.

It is experimentally challenging but worthwhile to continue to improve paradigms by modifying the tasks so that they are in accordance with the infant’s world. For example, presenting multimodal stimuli allowed the use of an unusually high number of trials for analysis, suggesting an advantage of multimodal over unimodal stimuli in capturing infants’ attention (Grossmann, Striano, & Friederici, 2006). This is of special interest when the generally low trial number of infant studies is considered. Moreover, a recent study employed a novel interactive paradigm to assess the neural correlates of joint attention in 9-month-old infants (Striano, Reid et al., 2006), and found that the amplitude of the elicited ERP component was substantially larger in this study than that seen in previous literature, which may be due to the use of a live interaction. The use of multimodal stimuli and interactive
paradigms has the advantage of increased social significance for the child and higher ecological validity when compared with those paradigms utilized in the past. Despite the advantages of using live interaction paradigms, we have to bear in mind that such paradigms also pose certain technical difficulties (e.g., complicated time control, increased motion artifacts).

Infant brain function has been predominantly investigated using EEG and ERPs. Although these methods have helped to understand the neural underpinnings of infant social cognition, they suffer from a relatively poor spatial resolution. Researchers have also begun to use fMRI to localize activity in the infant brain evoked by speech stimuli (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002), but fMRI requires rigid stabilization of the head and exposes infants to a noisy acoustic environment. These concerns make it unlikely that fMRI will be routinely used in paradigms with infants. A technique called near-infrared spectroscopy (NIRS) that permits the measurement of cerebral haemoglobin oxygenation in response to brain activation has been successfully used to study infant visual, language, and memory abilities (for a review, see Aslin & Mehler, 2005). This novel technique does not suffer from the same problems in its use with infants as fMRI and might therefore be a promising tool to study the infant social brain. Improving the tools used to localize functional activations in the infant brain is critical for our understanding of how the neural structures implicated in the adult social brain develop in early ontogeny.

Even once improved methods show us more clearly how neural events co-vary with infants’ processing of social stimuli, the interpretation of such data will remain a major theoretical challenge. First attempts have been made to test theories of functional brain development (Johnson, 2001) by examining which parts of what is thought to be the adult social brain network are already active in infants (Johnson et al., 2005). The results of these studies provide preliminary support for the interactive specialization view of human functional brain development, which assumes that developmental changes in the response
properties of cortical regions occur as they interact and compete with each other to acquire their functional role (Grossmann & Johnson, 2007). This is in contrast to the “maturational view” in which the maturation of specific regions of the cortex is related to newly emerging cognitive and social functions, and also in contrast to “skill learning,” which purports that structures in the social brain are engaged by social stimuli due to their role in perceptual expertise. Future work with the imaging methods described above will be necessary to determine which of these viewpoints most accurately reflects the emerging social brain network during the first years.

Another important issue is that although the cross-talk between developmental psychologists and social cognitive neuroscientists has begun on a theoretical level (Decety & Sommerville, 2004; Meltzoff & Decety, 2003), there is very little infant brain research that is more directly informed and motivated by already existing theories of infant social cognitive development (Csibra & Gergely, 2006; Meltzoff, 2002, 2005; Tomasello et al., 2005). The available theoretical frameworks explaining provide a rich source of hypotheses that are testable using neuroimaging tools. In this context it will be of particular importance to identify the neural processes that underlie known social behavioral and social cognitive transitions. With respect to the topic of gaze perception, the proposed behavioral transition from simple gaze following to more sophisticated joint attention (Tomasello & Carpenter, 2007) is one area that, in our view, deserves closer examination on a neural level. Together, all the points listed here underline the truly interdisciplinary nature of the emerging field of social neuroscience of infancy, and presents the field with the challenge of training scientists that are able to combine knowledge from cognitive neuroscience and developmental psychology in order to shed light on the developing social brain. It is our hope that this chapter will help to inform and guide future research.
References


Conty, L., N’Diaye, K., Tijus, C., & George, N. (in press). When eye creates the contact! ERP evidence for early dissociation between direct and averted gaze motion. *Neuropsychologia*.


Gamma oscillations respond differently than evoked potentials: an interleaved EEG-fMRI-study. BMC Neuroscience, 4, 22.


Menon, Farroni, Rigato, & Johnson. (in preparation). Constraints in the perception of facial expressions at birth.


Richards, J. E. (2004). Recovering dipole sources from scalp-recorded event-related-
potentials using component analysis: Principal component analysis and independent component analysis. *International Journal of Psychophysiology, 54*, 201-220


**Figure Captions**

*Table 1.* Overview of brain regions implicated in eye gaze processing in the human adult and their probable functional roles (note that this is not an exhaustive review of all neuroimaging studies available).

*Table 2.* Summary of our behavioral findings in newborns and electrophysiological findings in 4-month-olds.

*Figure 1.* Examples of direct and averted gaze stimuli used in our behavioral and electrophysiological studies.
<table>
<thead>
<tr>
<th>Brain Regions</th>
<th>Functional Properties</th>
<th>Studies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right Superior Temporal Sulcus (STS)</td>
<td><strong>Posterior STS:</strong> no clear preference for specific gaze direction, sensitivity to others’ (signallers’) intentional states indicated by eye gaze</td>
<td>Calder et al. (2002)</td>
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<tr>
<td></td>
<td><strong>Anterior STS:</strong> dissociaible coding of different gaze directions (left vs. right gaze)</td>
<td>Pelprey et al. (2003, 2004)</td>
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<td>Puce et al. (1998)</td>
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<td>Wicker et al. (1998)</td>
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<td>Calder et al. (2007)</td>
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<tr>
<td>Right Inferior Parietal Lobule (IPL)</td>
<td>general role in orienting attention which is initiated by viewing averted gaze</td>
<td>Calder et al. (2007)</td>
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<td></td>
<td></td>
<td>Hoffman &amp; Hasby (2000)</td>
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<tr>
<td>Medial Prefrontal Cortex (MPFC)</td>
<td>general role in mentalizing, detection and decoding of communicative/social intentions towards self (receiver) which can be triggered by gaze</td>
<td>Conty et al. (in press)</td>
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<td></td>
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<td>Bristow et al. (2007)</td>
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<td>Kampe et al. (2003)</td>
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<td>Schilbach et al. (2006)</td>
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<tr>
<td>Amygdala</td>
<td>extraction of affective significance, more responsive to direct gaze</td>
<td>George et al. (2001)</td>
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<tr>
<td>Fusiform Face Area (FFA)</td>
<td>enhanced face encoding of direct gaze faces, functional coupling with amygdala</td>
<td>Kawashima et al. (1999)</td>
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<td>George et al. (2001)</td>
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<tr>
<td>Face</td>
<td>Newborns</td>
<td>4-month-olds</td>
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<tr>
<td></td>
<td>Behavior</td>
<td>ERPs</td>
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| upright | - direct gaze:  
      eye contact preference | - direct gaze:  
      enhanced N290 | - direct gaze:  
      enhanced occipital evoked gamma  
      prefrontal induced gamma |
|        |          |              | - averted gaze:  
      temporo-parietal induced gamma |
| inverted | No preference | No ERP differences | No gamma activity |
| oriented | No preference | - direct gaze:  
      enhanced N290 | - direct gaze:  
      occipital evoked gamma  
      temporo-parietal induced gamma |
A: Upright face  
B: Inverted face  
C: Oriented face