Social perception in the infant brain: gamma oscillatory activity in response to eye gaze

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Gamma band oscillatory brain activity was measured to examine the neural basis of 4-month-old infants' perception of eye gaze direction. Infants were presented with photographic images of upright and inverted female faces directing their gaze towards them or to the side. Direct gaze compared to averted gaze in upright faces elicited increased early evoked gamma activity at occipital channels indicating enhanced neural processing during the earliest steps of face encoding. Direct gaze also elicited a later induced gamma burst over right prefrontal channels, suggesting that eye contact detection might recruit very similar cortical regions as in adults. An induced gamma burst in response to averted gaze was observed over right posterior regions, which might reflect neural processes associated with shifting spatial attention. Inverted faces did not produce such effects, confirming that the gamma band oscillations observed in response to gaze direction are specific to upright faces. These data demonstrate the use of gamma band oscillations in examining the development of social perception and suggest an early specialization of brain regions known to process eye gaze.

Keywords: social perception; eye gaze; development; gamma oscillations; infancy

INTRODUCTION

The detection and monitoring of eye gaze direction is thought to be essential for effective social learning and communication among humans (Bloom, 2000; Kampe et al., 2003; Csibra and 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). A sensitivity to eye contact is evident early in human ontogeny. From birth, infants prefer to look at faces with their eyes open (Batki et al., 2000), and they also look longer at faces that engage them in mutual gaze when compared to averted gaze (Farroni et al., 2002). Another important aspect of eye gaze processing is that averted gaze may trigger a reflexive shift of an observer's visual attention (Driver et al., 1999). Newborns have been found to be faster in making saccades to peripheral targets cued by the direction of eye movements suggesting a rudimentary form of gaze following (Farroni et al., 2004b). It has been argued that an early sensitivity to both aspects of eye gaze serves as a major foundation for later development of social skills (Baron-Cohen, 1995; Hood et al., 1998; Csibra and Gergely, 2006). Given the important role of eye gaze perception for human social interactions, the question arises how the behaviorally expressed sensitivity for mutual gaze and the capacity to follow gaze are implemented in the infant brain, and to what extent is this similar to that seen in adults.

Farroni et al. (2002) measured 4-month-old infants' event-related potentials (ERPs) to examine neural processing of faces when accompanied with direct or averted gaze. In this study, an ERP component (N170/N290) known to be sensitive to faces in adults (Bentin et al., 1996) and infants (de Haan et al., 2002; Halit et al., 2003, 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 in a follow-up ERP study (Farroni et al., 2004a) in which 4-month-olds showed an enhanced cortical processing of direct gaze even when the head was averted. 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 et al., 2004), which had been successfully employed to localize sources of infant electrophysiological recordings (Richards, 2004, 2005). Johnson et al. (2005) identified brain sources in 4-month-old infants' right temporal cortex (specifically in the fusiform gyrus) discriminating between direct and averted gaze. 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 medial fronto-polar regions of pre-frontal cortex. 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). Such an effect was not revealed in traditional ERP analyses, illustrating the power of statistical source separation methods (Makeig *et al.*, 2004).

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). It is thought that such brain oscillations in the high frequency range reflect neural mechanisms by which activity of small neuronal networks is synchronized, whereas very large networks are recruited during slow oscillations (Buzsaki and Draguhn, 2004). Synchronous activity of oscillating networks is a prominent feature of neural activity throughout the animal kingdom (Sejnowski and Paulsen, 2006), and it is viewed as the critical middle ground linking single-neuron activity to behavior (Engel *et al.*, 2001; Herrmann *et al.*, 2004). More specifically, gamma 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 its 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 and Bertrand, 1999; Csibra and Johnson, 2007).

As a theoretical framework, which attempts to assign functional significance to early evoked and late induced gamma-band responses, Herrmann *et al.* (2004) have put forward a Match-Utilization-Model (MUM). According to this model, the early gamma-band response reflects the matching of stimulus-related information with memory contents in primary sensory cortex. Once a stimulus has been identified through this matching stage, this information can be used in all kinds of more complex cognitive operations involving other brain areas and the late induced gamma response might be a signature of such a utilization process.

Gamma oscillations are also of special interest because they have been found to correlate with the BOLD response measured by fMRI as shown in invasive work with animals (Niessing *et al.*, 2005) and non-invasive studies combining EEG and fMRI in humans (Foucher *et al.*, 2003; Fiebach *et al.*, 2005). It has also been shown that whereas the BOLD signal correlated with gamma-band activity, such a correlation was not found for ERP measures (Foucher *et al.*, 2003). These findings are consistent with a biophysical model, which suggests that increases in hemodynamic signals as measured by fMRI are associated with a shift in the spectral mass from low to high frequencies as measured with EEG (Kilner *et al.*, 2005). Gamma oscillatory activity in infants has so far only been studied in the context of object processing (Csibra *et al.*, 2000; Kaufman *et al.*, 2003, 2005).

The current study examined gamma oscillations and its relationship to eye gaze perception in 4-month-old infants. We predicted a burst of gamma oscillation over prefrontal sites to direct gaze if it is 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 (Hood *et al.*, 1998; Farroni *et al.*, 2003). The right intraparietal sulcus (IPS) and right superior temporal sulcus (STS) identified as sensitive to averted gaze in the adult brain (Hofman and 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, which is thought to disrupt configural face processing (Rodriguez *et al.*, 1999; Turati *et al.*, 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.

METHOD

Participants

The final sample in the group which viewed upright faces consisted of 12 4-month-old infants (five females) taken from Experiment 2 of Farroni *et al.*'s (2002) study, aged between 124 and 143 days ($M = 132$ days, s.d. $= 7$ days). Three infants from the previously published data set were excluded from the analyses, in order to avoid contamination of the data with possible eye movement artefacts particularly at frontal channels. The final sample in the group which viewed inverted faces consisted of twelve 4-month-old infants (five females) taken from Experiment 2 of Farroni *et al.*'s (2004a) study, aged between 120 and 150 days ($M = 135$ days, s.d. $= 8$ days).

Stimuli

The stimuli were digitized colour photographic images of female faces directing their gaze straight on to the viewers (direct gaze) or averted to one side (averted gaze). The visual angle subtended $41.3° \times 27.2°$, and each eye subtended $3.0° \times 5.1°$.

Procedure

Infants sat on their parent's lap 60 cm from a 40×29 cm computer monitor within an acoustically and electrically shielded, dimly lit room. A video camera centred on the infant's face allowed us to record her/his gaze.

Their attention was drawn to the middle of the screen by a dynamic colour cartoon. When they fixated it the stimulus froze for 800–1200 ms before a face replaced it for 1000 ms. Faces with direct and averted gaze were presented in a random order and with equal probability for as long as the babies were willing to look at them. Infants who were included in the final sample typically completed a total of 50–150 trials.

EEG measurement and data analysis

The brain electrical activity was recorded by using a Geodesic Sensor Net consisting of 62 electrodes evenly distributed across the scalp and the vertex lead serving as a reference (Tucker, 1993). The electrical potential was amplified with 0.1–100 Hz bandpass, digitized at 250 Hz sampling rate. Artifacts caused by eye and body movements were eliminated by manual rejection. In addition, the infants' visual behavior was coded from videotape, and trials during which the infant did not fixate the screen during stimulation were excluded from further analysis. Participants who were included in the final sample contributed at least 18 trials per condition [mean number of trials: 33.4 (upright face/direct gaze); 32.8 (upright face/averted gaze); 28.2 (inverted face/direct gaze); 30.8 (inverted face/averted gaze)]. Induced gamma oscillations were analyzed using an established procedure (Csibra et al., 2000; Kaufman et al., 2003, 2005) in which we applied a continuous wavelet transformation to single trials of EEGs in each channel, using Morlet wavelets at 1 Hz intervals. The wavelet transformation was performed on 1200 ms long EEG segments (200 ms prestimulus onset and 1000 ms poststimulus onset). EEG data for 100 ms at the beginning and at the end of each segments had to be removed due to the distortion in the time-frequency decomposition commonly caused by wavelets. The average amplitude during the 100 ms prestimulus interval was considered as the baseline and was subtracted from the whole time-varying signal. We also assessed evoked gamma oscillatory activity (Tallon-Baudry and Bertrand, 1999; Csibra et al., 2000; Csibra and Johnson, 2007) by applying the same Morlet wavelets to the averaged ERPs.

Based on the visual inspection of the data, which revealed that in correspondence with previous findings with adults (e.g. Busch et al., 2006), evoked gamma effects were observed between 20 and 40 Hz and induced gamma effects between 40 and 60 Hz, we divided the gamma band into lower (20–40 Hz) and higher (40–60 Hz) gamma and examined the mean amplitude in 100 ms blocks (50–150 ms, 150–250 ms, 250–350 ms, 350–450 ms) to assess the gamma oscillation effects statistically. In order to rule out that the effects observed were due to differences before stimulus onset, we also tested whether there were any statistical differences between conditions during the baseline period (-100–0 ms), which was tested by comparing the baseline activity between conditions before we applied the baseline correction. Based on our hypothesis and on prior findings (Farroni et al., 2002;

Johnson et al., 2005), repeated measures analysis of variance (ANOVAs) were conducted for three different scalp locations. (i) At occipital channels (35, 36, 38, 39, 43) mean amplitude of the evoked oscillations was evaluated by ANOVAs with gaze direction (direct × averted) as a within subject factor and face orientation as a between subject factor (upright × inverted). Occipital channels were chosen on the basis of the maximum of ERP effects observed in the previous ERP study (Farroni et al., 2002). At (ii) prefrontal (1, 2, 3, 6, 8, 10, 11, 12, 13, 62) and at (iii) posterior [lateral occipital, temporal and parietal (28, 29, 32, 33, 34, 36, 37, 39, 40, 41, 44, 45)] channels, mean amplitude was assessed by ANOVAs with gaze direction (direct × averted) and lateralization (left × right) as a within subject factor, and face orientation as a between subject factor (upright × inverted). Lateralization was used as an additional factor in these analyses because visual inspection revealed a clear lateralization of the effects. One-sample t-tests were used to determine whether the observed gamma-band oscillations were significantly different from baseline.

RESULTS

Early occipital evoked gamma activation

A repeated measures ANOVA revealed a significant interaction between gaze direction and face orientation ($F[1,22] = 4.773$, $P = 0.04$) and a significant main effect of face orientation ($F[1,22] = 5.243$, $P = 0.032$) in the lower gamma band (20–40 Hz) observed over occipital channels (the channel locations correspond to the area around O1 and O2 of the 10–20 system) in the time window from 50 to 150 ms. As shown in Figure 1, in the context of the upright face, evoked gamma activity was larger in response to direct gaze when compared to averted gaze (paired sample t-test: $t[11] = 2.461$, $P = 0.032$), whereas gamma band responses to inverted faces did not differ from each other. The mean amplitude for upright faces was significantly larger for upright than for inverted faces (independent-sample $t[22] = 2.258$, $P = 0.0342$). One sample t-tests revealed that evoked gamma band responses to all stimuli were significantly different from baseline (upright face/direct gaze: $t[11] = 3.895$, $P = 0.002$; upright face/averted gaze: $t[11] = 3.245$, $P = 0.0078$; inverted face/direct gaze: $t[11] = 2.324$, $P = 0.0403$; inverted face/averted gaze: $t[11] = 2.245$, $P = 0.0463$).

Late right prefrontal induced gamma activation

A repeated measures ANOVA revealed a significant interaction between gaze direction, lateralization and face orientation for induced gamma activity observed over prefrontal channels in the time window from 250 to 350 ms in the higher gamma band (40–60 Hz), $F(1, 22) = 4.884$, $P = 0.038$. As shown in Figure 2A, the analyses indicated that direct gaze in the context of an upright face elicited a significant gamma burst over right prefrontal channels (the channel locations correspond to the area between Fp2 and F4 of the
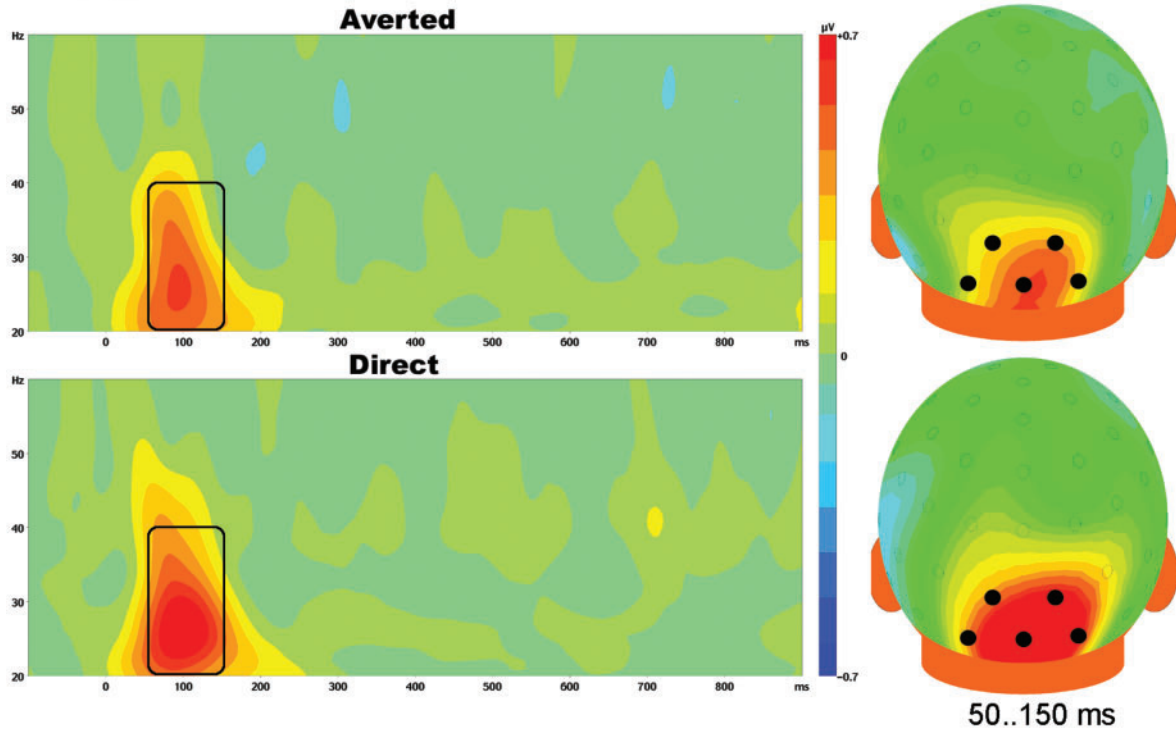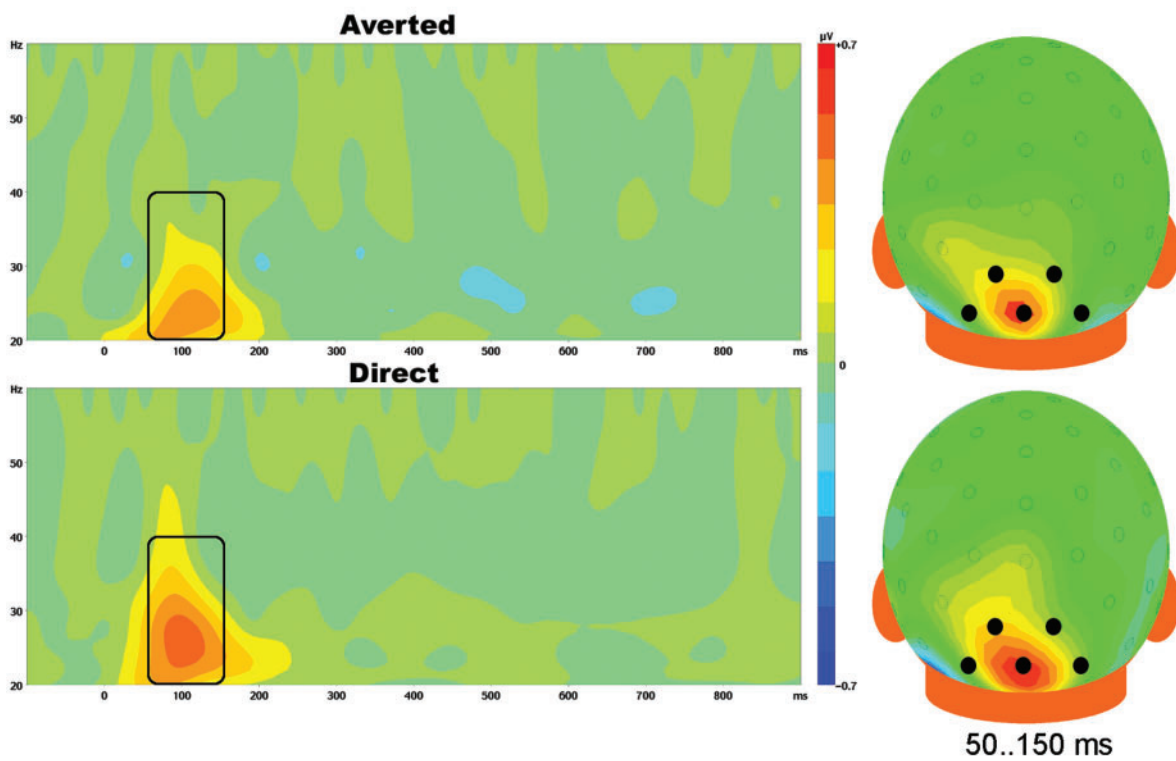
Fig. 1 Evoked (phase-locked) gamma-band (20–60 Hz) EEG responses to averted and direct gaze. The time-frequency plot represents the average amplitude of oscillatory activation measured at the five occipital electrodes marked on the scalp surface maps (right). The rectangles in the time-frequency plots indicate the gamma bursts that were significantly different from baseline. A: Upright face condition, B: Inverted face condition.
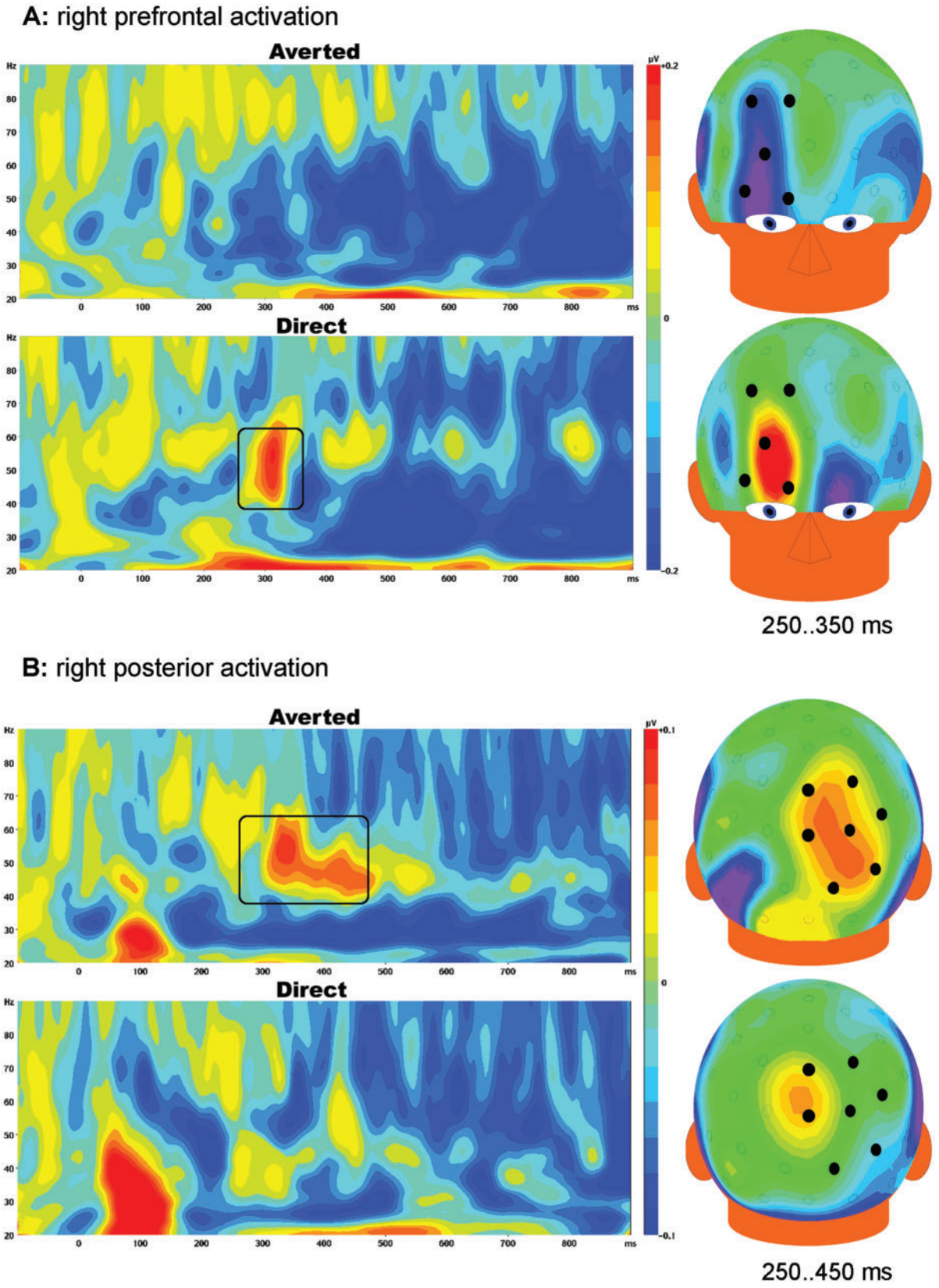
Fig. 2 Induced gamma-band (20–90 Hz) EEG responses to averted and direct gaze in the context of an upright face. The time-frequency plots represent the average oscillatory activity measured at electrodes over the right hemisphere marked on the scalp surface maps (right). A: Prefrontal activation, B: Posterior activation.

10–20 system), one sample $t[11] = 2.54$, $P = 0.027$. This was the only condition significantly different from baseline. Paired sample t-tests showed that gamma activity in this time window differed significantly between direct and averted gaze in the upright face condition over right prefrontal channels ($t[11] = 2.465$, $P = 0.031$).

Late right occipito–temporal–parietal induced gamma activation

The ANOVA revealed a significant interaction between gaze direction, lateralization and face orientation for the gamma activity observed over occipital, temporal and parietal (posterior) channels across the time windows from 250 to 350 ms ($F[1, 22] = 6.243$, $P = 0.0204$) and 350 to 450 ms ($F[1, 22] = 5.257$, $P = 0.0318$). As shown in Figure 2B, only averted gaze elicited a gamma burst over right posterior channels (these channels location correspond to the O2- Pz–T8 triangle of the 10–20 system), one sample: $t[11] = 2.96$, $P = 0.013$. This was the only condition significantly different from baseline. Paired sample t-tests showed that gamma activity in this time window differed significantly between averted and direct gaze for upright faces over the right hemisphere ($t[11] = 2.57$, $P = 0.026$).

DISCUSSION

In the current study, we used gamma oscillatory measures to examine 4-month-old infants' neural processing 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, 2004a; 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 stronger early gamma activity (20–40 Hz) at occipital channels. It is interesting to note that the modulation of the evoked gamma response in the current study was observed much earlier (100 ms) than the effect in the previous ERP studies (290 ms, Farroni *et al.*, 2002, 2004a). This indicates that evoked gamma activity is a more sensitive measure than ERPs of some aspects of early cortical processes related to the discrimination of gaze direction. 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 and Betrand, 1999). In adults, it has been shown that evoked gamma activity is significantly larger for items that match memory representations (Herrmann *et al.*, 2003; Herrmann *et al.*, 2004). It is possible that for infants a face with direct gaze represents a more familiar or more prototypical face configuration (Farroni *et al.*, 2006) 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 (Farroni *et al.*, 2007) of upright faces with direct gaze in infants.

As predicted, direct gaze also elicited a late induced gamma burst over right prefrontal channels. In a previous analysis based on ICA, cortical sources sensitive to gaze direction had been identified in fronto-polar regions (Johnson *et al.*, 2005), which is consistent with the present 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 right 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). Interestingly, a similar activation in the right MPFC has been reported when calling the person's name, indicating that ostensive signals independent of modality elicit common activations in this brain area (Kampe *et al.*, 2003). It is important to note that gamma oscillations measured with EEG have been found to correlate with the BOLD response used in fMRI (Foucher *et al.*, 2003; Niessing *et al.*, 2005; Fiebach *et al.*, 2005). It is thus possible that eye contact detection in 4-month-old infants recruits very similar brain mechanisms as in adults. The gamma burst distributed over right frontal cortex in infants might reflect less localized functional activity than in adults, which is consistent with the view that characterizes functional brain development by increasing specialization and localization (Johnson, 2001). Alternatively, it has been found that emotional processing, regardless of valence, enhanced gamma band power at right frontal electrodes in adults (Müller *et al.*, 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 (Hood *et al.*, 1998; Farroni *et al.*, 2000, 2003). The right IPS and right STS have been identified as sensitive to averted gaze in the adult human brain (Haxby *et al.*, 2000; Hofman and Haxby, 2000). 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 gamma burst in response to averted gaze over right occipito–temporal–parietal regions might reflect similar but perhaps more diffuse brain activations in infants.

More generally, the lateralization of both induced gamma band effects to averted and to direct gaze to the right hemisphere might be due to the fact that (i) 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, and/or (ii) eye gaze perception triggers emotional processes in the infant, which have been shown to results 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 from upright faces. It further shows that the 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 important to note that the current findings show a high degree of correspondence in terms of timing and frequency content with previous findings in adults (Tallon-Baudry and Bertrand, 1999; Busch *et al.*, 2006). Namely, in agreement with the adult work, we observed early (around 100 ms) evoked gamma responses in the lower gamma band (20–40 Hz) and late (around 300 ms) induced responses in the higher gamma band (40–60 Hz). This suggests continuity throughout development, and further underlines the functional importance of gamma band oscillations. The current results also support recent accounts assigning functional significance to gamma band responses. Namely, as proposed in the MUM model (Herrmann *et al.*, 2004), evoked responses seem to reflect early brain processes related to 'matching' input to memory representations in sensory (visual) cortex, whereas late induced responses may indicate the 'utilization' of more complex cognitive brain processes in association corticies related to eye contact detection (direct gaze) and shifting spatial attention (averted gaze). Furthermore, recent work emphasized the relevance of long-distance synchronization across EEG electrodes for face perception indicating the integration of information from distant brain regions (Rodriguez *et al.*, 1999). Thus, in future studies it will be important to use measures of coherence or phase-synchrony (Herrmann *et al.*, 2005) in order to better understand the possible coupling of distant neuronal events of the gamma band effects observed here.

The current study identified different electrophysiological responses with distinct topographies for direct or averted gaze processing, which correspond to previous neuroimaging findings looking at gaze perception in adults. This suggests a relatively early specialization of the network of cortical structures involved in the perception of gaze direction. Having this network functional early in life may be critical for social communication and learning from others.

Conflict of Interest
None declared.

REFERENCES

Baron-Cohen, S. (1995). *Mindblindness: an essay on autism and theory of mind*. Cambridge, MA: MIT Press.

Batki, A., Baron-Cohen, S., Wheelwright, S., Connellan, J., Ahluwalia, J. (2000). Is there an innate gaze module? Evidence from human neonates. *Infant Behavior & Development*, 23, 223–9.

Bentin, S., Allison, T., Puce, A., Perez, A., McCarthy, A. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8, 551–65.

Bloom, P. (2000). *How children learn the meanings of words*. Cambridge, MA: MIT Press.

Busch, N.A., Herrmann, C.S., Müller, M.M., Lenz, D., Gruber, T (2006). A cross-laboratory study of event-related gamma activity in a standard object-recognition paradigm. *Neuroimage*, 33, 1169–77.

Buzsaki, G., Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science*, 304, 1926–9.

Csibra, G., Davis, G., Spratling, M.W., Johnson, M.H. (2000). Gamma oscillations and object processing in the infant brain. *Science*, 290, 1582–5.

Csibra, G., Gergely, G. (2006). Social learning and social cogniton: the case for pedagogy. In: Munakata, Y., Johnson, M.H., editors. *Processes of Change in Brain and Cognitive Development. Attention and Performance XXI*. Oxford: Oxford University Press, pp. 249–74.

Csibra, G., Johnson, M.H. (2007). Investigating event-related oscillations in infancy. In: de Haan, M., editor. *Infant EEG and Event-Related Potentials*. Hove, England: Psychology Press, pp. 289–304.

de Haan, M., Pascalis, O., Johnson, M.H. (2002). Specialization of neural mechanisms underlying face recognition in human infants. *Journal of Cognitive Neuroscience*, 14, 199–209.

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition*, 6, 509–40.

Engel, A.K., Fries, P., Singer, W. (2001). Dynamic predictions: oscillations and synchrony in top-down processing. *Nature Reviews Neuroscience*, 2, 704–16.

Farroni, T., Csibra, G., Simion, F., Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proceedings of National Academy of Science (USA)*, 99, 9602–5.

Farroni, T., Johnson, M.H., Csibra, G. (2004a). Mechanisms of eye gaze perception during infancy. *Journal of Cognitive Neuroscience*, 16, 1320–6.

Farroni, T., Mansfield, E.M., Lai, C., Johnson, M.H. (2003). Infants perceiving and acting on the eyes: tests of an evolutionary hypothesis. *Journal of Experimental Child Psychology*, 85, 199–212.

Farroni, T., Massaccesi, S., Menon, E., Johnson, M.H. (2007). Direct gaze modulates face recognition in young infants. *Cognition*, 102, 396–404.

Farroni, T., Menon, E., Johnson, M.H. (2006). Factors' influencing newborns' preferences for faces with eye contact. *Journal of Experimental Child Psychology*, 95, 298–308.

Farroni, T., Pividori, D., Simion, F., Massaccesi, S., Johnson, M.H. (2004b). Eye gaze cueing of attention in newborns. *Infancy*, 5, 39–60.

Fiebach, C.J., Gruber, T., Supp, G. (2005). Neuronal meachanisms of repetition priming in occipitotemporal cortex: spatiotemporal evidence

from functional magnetic imaging and electroencephalography. *Journal of Neuroscience*, 25, 3414–22.

Foucher, J.R., Otzenberger, H., Gounot, D. (2003). The BOLD response and the gamma oscillations respond differently than evoked potentials: an interleaved EEG-fMRI study. *BMC Neuroscience*, 4, 22.

Halit, H., Csibra, G., Volein, A., Johnson, M.H. (2004). Face-sensitive cortical processing in early infancy. *Journal of Child Psychology and Psychiatry*, 45, 1228–34.

Halit, H., de Haan, M., Johnson, M.H. (2003). Cortical specialization for face processing: Face-sensitive event-related potential components in 3- and 12-month-old infants. *NeuroImage*, 19, 1180–93.

Haxby, J.V., Hoffman, E., Gobbini, M.I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4, 223–33.

Herrmann, C.S., Grigutsch, M., Busch, N. (2005). EEG oscillations and wavelet analysis. In: Handy, T.C., editor. *Event Related Potentials: A Methods Handbook*. Cambridge: MIT Press, pp. 263–99.

Herrmann, C.S., Lenz, D., Junge, S., Busch, N.A., Maess, B. (2003). Memory-matches evoke human gamma-responses. *BMC Neuroscience*, 5, 13.

Herrmann, C.S., Munk, M.H.J., Engel, A.K. (2004). Cognitive functions of gamma-band activity: memory match and utilization. *Trends in Cognitive Sciences*, 8, 347–55.

Hoffman, E.A., Haxby, J.V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, 3, 80–4.

Hood, B.M., Willen, J.D., Driver, J. (1998). Adults eyes trigger shifts of visual attention in human infants. *Psychological Science*, 9, 131–4.

Johnson, M.H. (2001). Functional brain development in humans. *Nature Reviews Neuroscience*, 2, 475–83.

Johnson, M.H., Griffin, R., Csibra, G., et al. (2005). The emergence of the social brain network: evidence from typical and atypical development. *Development and Psychopathology*, 17, 599–619.

Kampe, K., Frith, C.D., Frith, U. (2003). 'Hey John': signals conveying communicative intention toward self activate brain regions associated with 'mentalizing,' regardless of modality. *Journal of Neuroscience*, 12, 5258–63.

Kaufman, J., Csibra, G., Johnson, M.H. (2003). Representing occluded objects in the human infant brain. *Proceedings of the Royal Society B: Biological Sciences*, 270/S2, 140–3.

Kaufman, J., Csibra, G., Johnson, M.H. (2005). Oscillatory activity in the infant brain reflects object maintenance. *Proceedings of the National Academy of Sciences USA*, 102, 15271–4.

Kilner, J.M., Mattout, J., Henson, R., Friston, K.J. (2005). Hemodynamic correlates of EEG: a heuristic. *NeuroImage*, 280, 280–6.

Makeig, S., Debener, S., Onton, J., Delrome, A. (2004). Mining event-related brain dynamics. *Trends in Cognitive Sciences*, 18, 204–10.

Müller, M., Keil, A., Gruber, T., Elbert, T. (1999). Processing of affective pictures modulates right-hemispheric gamma band activity. *Clinical Neurophysiology*, 110, 1913–20.

Niessing, J., Ebisch, B., Schmidt, K.E., Niessing, M., Singer, W., Galuske, R.A.W. (2005). Hemodynamic signals correlate tightly with synchronized gamma oscillations. *Science*, 309, 948–51.

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, 201–20.

Richards, J.E. (2005). Localizing cortical sources of event-related potentials in infants' covert orienting. *Developmental Science*, 8, 255–78.

Rodriguez, E., George, N., Lachaux, J.P., Martinere, J., Renault, B., Varela, F. (1999). Perception's shadow: long-distance synchronization of human brain activity. *Nature*, 397, 430–3.

Schilbach, L., Wohlschläger, A.M., Newen, A., et al. (2006). 'Being with virtual others': neural correlates of social interaction. *Neuropsychologia*, 44, 718–30.

Sejnowksi, T. J., Paulsen, O. (2006). Network oscillations: emerging computational principles. *Journal of Neuroscience*, 26, 1673–6.

Tallon-Baudry, C., Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences*, 3, 151–62.

Tucker, D. (1993). Spatial sampling of head electrical fields: the geodesic sensor net. *Electroencephalography and Clinical Neurophysiology*, 87, 154–63.

Turati, C., Sangrioli, S., Ruel, J., de Schonen, S. (2004). Evidence of the face inversion effect in 4-month-old infants. *Infancy*, 6, 275–97.