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Mechanisms of Eye Gaze Perception during Infancy

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Abstract

■ Previous work has shown that infants are sensitive to the direction of gaze of another's face, and that gaze direction can cue attention. The present study replicates and extends results on the ERP correlates of gaze processing in 4-month-olds. In two experiments, we recorded ERPs while 4-month-olds viewed di-

rect and averted gaze within the context of averted and inverted heads. Our results support the previous finding that cortical processing of faces in infants is enhanced when accompanied by direct gaze. However, this effect is only found when eyes are presented within the context of an upright face. ■

INTRODUCTION

Faces are salient stimuli to typically developing individuals from the very earliest stages of postnatal development (Valenza, Simion, Macchi Cassia, & Umiltà, 1996; Johnson & Morton, 1991; Goren, Sarty, & Wu, 1975). Faces also provide social information on identity (Bruce & Young, 1986), focus of attention (Langton, Watt, & Bruce, 2000), intentions (Baron-Cohen, 1995), and emotional state (Ekman, 1982) during interpersonal communication. Of all the facial features, the eyes appear to be particularly important (Emery, 2000; Langton et al., 2000). As early as the second month of life, the eyes become the most scanned internal feature of faces (Maurer, 1985; Haith, Bergman, & Moore, 1977), a bias that continues to adulthood (Walker-Smith, Gale, & Findlay, 1977; Noton & Stark, 1971) except in schizophrenia (Phillips & Davis, 1997) and autism (Pelphrey et al., 2002). Recently, Farroni, Johnson, Brockbank, and Simion (2002) have shown that even newborns preferentially look toward faces with direct gaze. This finding reinforces the views that emphasize the importance of eye contact for successful social development (Kleinke, 1986). The ability to detect the direction of gaze of another's face is thought to be particularly important in guiding social interactions, and also emerges early in ontogeny (see Farroni, Mansfield, Lai, & Johnson, 2003 for a review). Several recent studies with adults have demonstrated that the direction of gaze of a face can cue visuospatial orienting in a viewer (Driver et al., 1999; Langton & Bruce, 1999; Friesen & Kingstone, 1998). In other words, adults are faster to respond to targets presented in locations congruent with the direction of eye gaze of a centrally presented face. This line of research has also been extended to infants and it has been demonstrated that human infants are able to fol-

low an adults' direction of gaze at 3–4 months (Farroni, Johnson, Brockbank, & Simion, 2000; Hood, Willen, & Driver, 1998) or even earlier (Farroni, Pividori, Simion, Massaccesi, & Johnson, 2004). Furthermore, it has been demonstrated that it is only following a period of mutual gaze with an upright face that cueing effects are observed in infants (Farroni et al., 2003).

With regard to the brain basis of eye gaze processing in adults, functional imaging studies have revealed a network of cortical areas that are activated during the processing of eye gaze. For example, Puce, Allison, Bentin, Gore, and McCarthy (1998) ran an fMRI experiment in which adult participants viewed moving eyes, moving mouths, or movements of checkerboard patterns. The results of this study showed that while all three conditions activated the motion area MT/V5, only moving eyes and mouths activated the superior temporal sulcus (STS). These results suggest that the STS is preferentially involved in the perception of gaze direction and mouth movements, but not to nonbiological motion. An MEG study by Watanabe, Kakigi, and Puce (2001) found similar results.

Because eyes always occur within the context of a face, another issue is the extent of overlap between the brain basis of eye gaze perception and the regions activated by face processing in general. To address this question Wicker, Michel, Henaff, and Decety (1998) used PET to study the pattern of cortical activation resulting from direct (mutual) eye gaze. They contrasted four experimental conditions: a face with neutral gaze, a face with averted gaze (to the right or left), a face with direction of gaze not visible, and a control condition in which participants kept their own eyes closed. The results were that in all three experimental conditions, regardless of direction of gaze, areas related to face processing were activated. These areas included the occipital pole (striate and extrastriate visual cortex) and the occipito-temporal areas, particularly in the right hemisphere. In addition to

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these regions, other brain regions were activated by processing direction of gaze, including the occipital part of the fusiform gyrus, the right parietal lobule, the right inferior temporal gyrus, and the middle temporal gyrus in both hemispheres. At the subcortical level, there was activation in the right amygdala, the right pulvinar, and bilaterally in the middle dorsal thalamic nucleus. This study suggests that the processing of eye gaze is controlled by a distributed network of brain areas overlapping with that involved in general face processing. This conclusion is also supported by an fMRI study by George, Driver, and Dolan (2001), who investigated how gaze direction (direct or averted) influences face processing using a gender recognition task. They presented a face with direct or averted gaze, and the face was either a frontal view or tilted at 45°. They observed that specific regions of the fusiform gyrus yielded stronger responses to faces when these looked directly at the subject (regardless the orientation of the head). This suggests that there may be deeper encoding of faces when gaze is directed at the observer.

To investigate the neurodevelopment of eye gaze processing, Farroni et al. (2002) recorded event-related brain potentials (ERPs) from 4-month-old infants, and found enhanced cortical processing of faces when accompanied by direct gaze. In particular, they found a difference between the two gaze directions at the time and scalp location of a known face-sensitive component of the infant ERP (“infant N170,” de Haan, Pascalis, & Johnson, 2002). This component of the infant ERP is thought to be the equivalent of a well-studied adult face-sensitive component, and in infants is sensitive to changes in the orientation and species of a face, at least by 12 months of age (Halit, de Haan, & Johnson, 2003). The conclusion from their studies is that direct eye contact enhances the perceptual processing of faces in

4-month-old infants. This suggests a fast mechanism of gaze direction analysis that may precede the full processing of faces.

EXPERIMENT 1

In Experiment 1, we attempted to replicate and extend the findings of Farroni et al. (2002). The specific question we addressed was whether the cortical processing of faces is modulated by gaze direction in the context of an averted head. Accordingly, we measured brain electrical activity of 4-month-old infants while they watched faces oriented 45° to the left or right (Figure 1). The ability to extract gaze direction under these circumstances would suggest a more sophisticated mechanism of gaze sensitivity comparable to that observed in adults.

In our analyses, as in Experiment 2 in Farroni et al. (2002), we focused on an ERP component known to be sensitive to faces (N170) (Bentin, Allison, Puce, Perez, & McCarthy, 1996, in adults; and de Haan et al., 2002, in infants), which is the first negative-going deflection after the P1 over posterior sides. As in previous studies with infants (de Haan et al., 2002), the “infant N170” component peaked around 240 msec poststimulus and, in contrast to the adult N170, was more medially distributed. Its amplitude was higher in response to direct gaze than to averted gaze (see Figure 2). The 12 occipital electrodes were collapsed into three lateral groups (left, medial, right) and a two-way ANOVA (laterality vs. stimulus type) was calculated on the average ERP amplitude within the 200–280 msec latency range.

Results and Discussion

A three-way ANOVA (Laterality × Gaze direction × Head orientation) was calculated on the average ERP ampli-

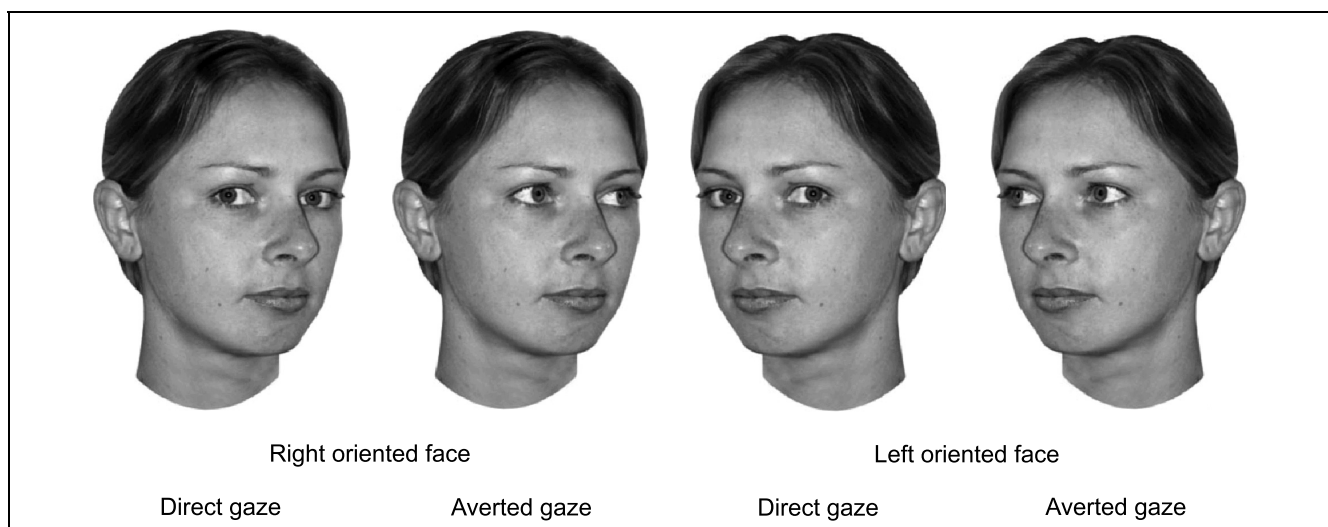
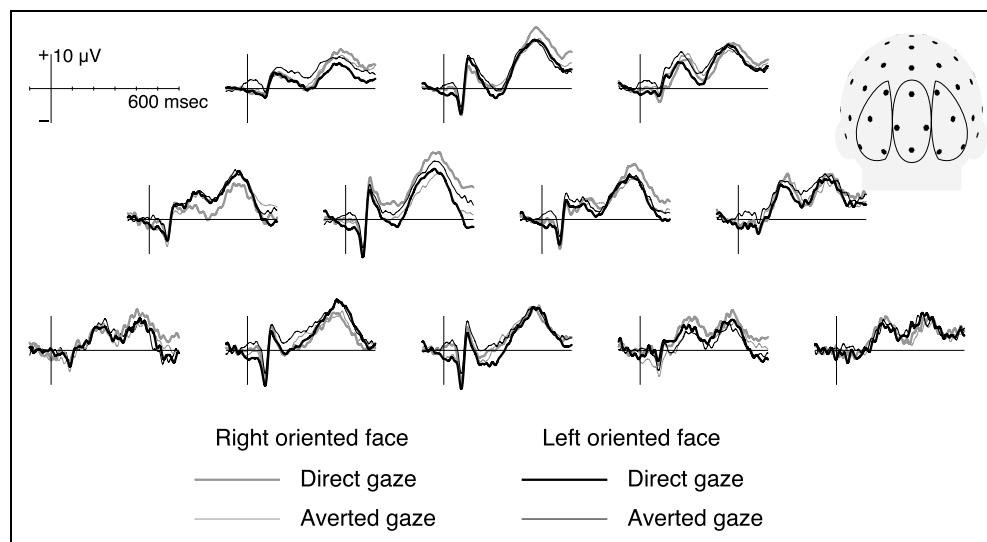


Figure 1. Examples of the stimuli in Experiment 1.

Figure 2. (A) ERPs in Experiment 1 at the 12 occipital recording sites that were included in the statistical analyses. The schematic head in the upper right corner indicates the electrode positions and the way they were collapsed into three groups for analysis. (B) Amplitude of the N240 component (average voltage in the 200–280 msec window) as a function of head orientation, gaze direction, and laterality.



tude within the 200–280 msec latency range. As this analysis yielded a significant Head orientation \times Laterality interaction [$F(2,32) = 2.376, p < .05$], we normalized the data by vector scaling to avoid a potential confound described by McCarthy and Wood (1985).¹ The same type of analysis on the normalized data yielded a significant main effect of Gaze direction [$F(1,16) = 4.854, p < .05$], indicating more negative amplitude in response to faces with direct than with averted gaze. Additionally, the main effect of Laterality was also significant [$F(2,32) = 16.460, p < .001$] because, as in Farroni et al. (2002), the “infant N170” component was more negative medially than laterally. The Head orientation \times Laterality interaction remained significant after normalization [$F(2,32) = 4.613, p < .05$], because the right oriented faces elicited a bigger response over the left side, while the left oriented faces elicited a bigger response over the right occipital area. This interaction was probably due to the differential extent that these faces fell into the two hemifields (Figure 1) and is consistent with the observation that visual stimuli evoke stronger response contralateral to the stimulus location.

The results from this experiment represent a substantial replication of our ERP findings from infants viewing nonaverted heads (Farroni et al., 2002), and therefore allows us to conclude that, at least by 4 months, direct gaze enhances face processing even with averted head angles. This suggests a sophisticated gaze detection system that is able to extract direction of gaze from the surrounding context of an upright face, and indicates that the mechanisms of gaze processing at 4 months may be different from those observed earlier in development. For example, Farroni, Johnson, Zulian, and Csibra (Unpublished data) showed that changing head angle of a stimulus face disrupts the preference for direct gaze seen with a straight head. In their experi-

ment, newborns did not show significant differences in total looking time at the direct and at the averted gaze, and they did not orient more frequently to the direct gaze face than to the other. The results of the present experiment with 4-month-olds show that the strong preference for faces with direct gaze is dependent on the eyes being situated within the context of a straight-ahead face.

EXPERIMENT 2

The results of Experiment 1 replicated and extended those of Farroni et al. (2002), and were consistent with enhanced cortical processing of faces with direct gaze. However, it remains possible that low-level aspects of the stimuli, such as symmetry or local spatial frequency differences, could have contributed to the effects observed. Further, the importance of an upright face configuration in facilitating the processing of faces with direct gaze in infants is unknown, although it has been demonstrated that infants are cued by motion of the pupils of another’s gaze only in the context of an upright face (Farroni et al., 2003). Thus, in this experiment, we presented infants with the same faces that we used in Experiment 2 of Farroni et al. (2002) but turned them upside down (Figure 3).

Results and Discussion

As in Experiment 1 and in other studies with infants (Halit et al., 2003; de Haan et al., 2002; Farroni et al., 2002), the “infant N170” component peaked around 240 msec poststimulus, but in this experiment there was no difference in its amplitude in response to direct and averted gaze (Figure 4). We calculated a two-way ANOVA on the average ERP amplitude within the 200–280 msec latency range with the factors of Laterality (left, medial,

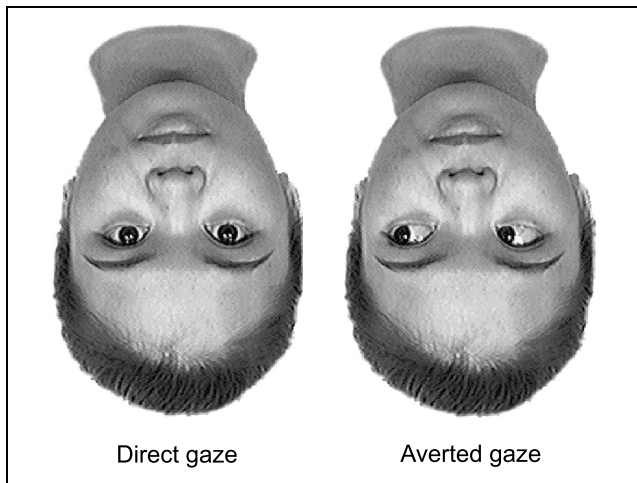


Figure 3. Examples of the stimuli in Experiment 2.

right) and Gaze direction (direct, averted). This analysis revealed no significant main effect of Gaze direction [$F(1,11) = 1.447, p > .05$], Laterality, or interaction between them.

Because identical testing conditions and stimuli were used in this experiment and in Experiment 2 of Farroni et al. (2002), a repeated-measures multivariate analysis of variance (MANOVA) was performed, with the between-subjects factor of Experiment (upright vs. inverted face), and the within-subjects factors of Gaze direction (direct vs. averted) and Laterality (right, medial, left). While the overall main effect of Gaze direction was not significant [$F(2,50) = 1.77, p > .05$], importantly, the interaction between Experiment and Gaze direction was highly significant [$F(1,25) = 7.925, p < .01$], demonstrating that the presence of an upright face context was required for triggering enhanced processing of direct gaze. The main effect of Laterality was also significant [$F(2,50) = 5.172, p < .01$], due to the “infant N170” amplitude being more negative over the medial than over the lateral leads in both experiments. Al-

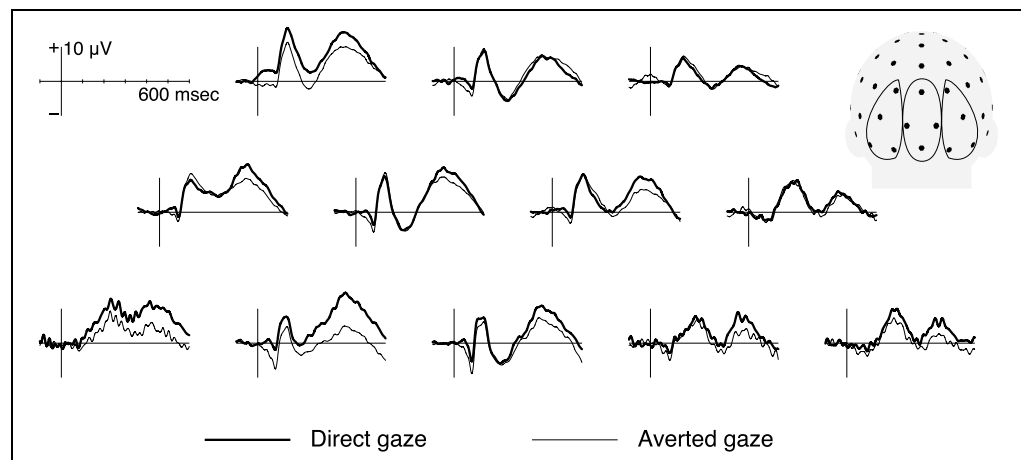
though there was no effect of gaze direction on the “infant N170” component in this experiment, Figure 3 suggests that there might have been such an effect on another face-sensitive component of the infant ERPs, the P400 (Halit et al., 2003; de Haan & Nelson, 1999; de Haan et al., 2002). A two-way ANOVA on the average amplitude of the 320–540 msec latency range, however, did not show a main effect of Gaze direction [$F(1,11) = 1.121, p > .05$], only an effect of Laterality [$F(2,22) = 4.415, p < .05$] due to the fact that the P400 was highest over the left, and lowest over the right occipital area.

GENERAL DISCUSSION

Three lines of evidence suggest that direct gaze (within the surrounding context of an upright face) has special status for the developing human brain. First, as reviewed earlier, several functional imaging studies with adults have established that some face-related areas of cortex are activated to a greater extent when accompanied by direct gaze (Kampe, Frith, & Frith, 2003; Frith & Frith, 1999). Second, behavioral studies have shown that newborns are sensitive to, and prefer to look at, faces that allow eye contact (direct gaze) (Farroni et al., 2002; Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000). Third, behavioral studies of eye gaze cueing in 4-month-olds have demonstrated that gaze shifts must be preceded by at least a short period of direct gaze (eye contact) to be effective as cues (Farroni et al., 2003). The results from the present article begin to bridge these three lines of evidence by demonstrating that there is facilitation of a face-related ERP component at 4 months of age. As in adult neuroimaging studies, direct gaze influences cortical processing even when the head itself is averted. Further, in accord with the infant gaze cueing studies, direct gaze is not effective when in the context of an inverted face.

The clear difference in ERP results obtained in Experiment 2 from that in Farroni et al. (2002) with 4-month-olds allows us to rule out symmetry and local spatial

Figure 4. (A) ERPs to the direct and averted gaze stimuli in Experiment 2 at the 12 occipital recording sites that were included in the statistical analyses. The schematic head in the upper right corner indicates the electrode positions and the way they were collapsed into three groups for analysis. (B) Amplitude of the N240 component (average voltage in the 200–280 msec window) as a function of gaze direction and laterality.



frequency as contributors to the gaze effect on the infant N170 with upright faces. Further, the difference in results suggests that direct gaze only facilitates face processing when the eyes are situated within the context of an upright face. However, this finding adds some complexity to earlier ERP results with infants showing that the infant N170 is not sensitive to face inversion at 3 and 6 months, but is sensitive by 12 months (Halit et al., 2003; de Haan et al., 2002). Specifically, while the infant N170 does differ between upright and inverted faces (both with direct gaze) until after 6 months, it is only modulated by direction of eye gaze when the face is presented upright. The finding from the present study therefore suggests some differential processing of upright and inverted faces at 4 months of age, although this is not detectable at the infant N170 when both faces presented have direct gaze. Further research is required to resolve this issue.

Recently, we have examined a possible behavioral evidence for importance of direct gaze for the development of the facial recognition and we have assessed whether, like older children and adults (Hood, Macrae, Cole-Davies, & Dias, 2003), the deeper encoding of faces when accompanied by direct gaze leads to better individual recognition (Farroni, Johnson, Massaccesi, & Züljan, in preparation). Specifically, we habituated groups of 4-month-old infants to individual faces with either direct gaze or averted gaze. We then assessed the extent of novelty preferences in a paired comparison test between the habituated face and a novel one. Infants that had been exposed to the face with direct gaze subsequently showed a stronger novelty preference in the test, providing evidence that they had encoded the habituation face more deeply. Time to habituation did not predict novelty preference, allowing us to rule out the simpler explanation that it is the longer looking time to faces with direct gaze that determines better processing. Rather, it seems that increased covert attention to, or deeper processing of, faces with direct gaze is the likely explanation.

The present study adds to a growing literature on social developmental cognitive neuroscience. Specifically, we propose that eye gaze processing shares largely overlapping neural processing with faces early in development. This is reflected in the enhancement of neural processing of faces when accompanied by direct gaze, and by the importance of direct gaze in allowing subsequent spatial attentional cueing and better individual recognition. With further development, we suggest that the neural processing of eye gaze and faces becomes more distinct. Consistent with these proposals is evidence that modulation of the N170 becomes less dependent on the eyes during childhood (de Haan, Johnson, & Halit, 2003; Taylor, 2003). Further, young children with autism show greater modulation of the N170 than do age-matched controls, raising the intriguing possibility that their eye gaze processing may be developmen-

tally delayed in the specific sense that it is more intertwined with general face processing. Such a view is consistent with the “interactive specialization” perspective on the development of the human social brain (Johnson, 2001, 2003).

METHODS

Participants

Infants were recruited from the Greater London area. All of them had been born at full term with no known complications. Informed consent was obtained from the parents. Thirty-one babies participated in Experiment 1. Fourteen of them were excluded because of excessive artifacts or completing too few trials (10), or because of fussiness (4). The final sample consisted of 8 female and 9 male infants, aged between 122 and 147 days ($M = 136$ days). Twenty-seven babies participated in Experiment 2. Fifteen of them were excluded because of excessive artifacts or completing too few trials (14), or because of fussiness (1). The final sample consisted of 5 female and 7 male infants, aged between 120 and 150 days ($M = 135$ days).

Apparatus and Stimuli

The infants sat on their parent's lap at 60 cm distance from a 40×29 cm ($36.9^\circ \times 27.2^\circ$) computer monitor within an acoustically and electrically shielded and dimly lit room. A video camera mounted below the monitor and centered on the infant's face allowed us to record his/her gaze. The stimuli were digitized color images of three static female faces presented at the center of the screen. In Experiment 1, the faces were oriented 45° either to the left or to the right, and their gaze was either directed in the same direction as the head (averted gaze) or towards the infants (direct gaze) (Figure 1). The oriented faces were aligned with the center of the screen so that the eye closer to the viewer appeared at location where the fixation stimuli had been presented. In Experiment 2, the faces were inverted upside down and each of the faces had two versions: one with a direct gaze, the other with averted gaze (Figure 3). The faces were aligned vertically so that the eyes appeared at the same height where the fixation stimuli were presented. The visual angle of the faces subtended to $21.2^\circ \times 13.8^\circ$ and one eye subtended to about $1.5^\circ \times 2.6^\circ$. Each trial began with the presentation of a static colorful fixation stimulus, which was presented for a variable 800–1200 msec duration. The face stimuli were presented for 1000 msec followed by 500 msec interval without visual stimulus. The trials were presented in a pseudorandom order in which the same gaze side (averted or straight) and head orientation (left or right) (Experiment 1) or, the same gaze side

(averted or straight) (Experiment 2) was not repeated more than three times in a row.

Procedure

After the baby was familiarized with the laboratory environment, the electrode net was mounted on the subject's head and fixed by elastic chinstraps. Then the infant sat in front of the stimulus monitor and his/her attention was attracted to the screen dynamic cartoons and sound stimuli. When the baby was attending the screen, trials were presented continuously. If the infant started to cry or became inattentive, the experiment was interrupted. Participants typically completed between 60 and 150 trials before the session was concluded.

EEG Recording and Data Analysis

The brain electric activity was measured simultaneously at 62 scalp locations by the infant version of the Geodesic Sensor Net (Tucker, 1993). The reference electrode was the vertex (Cz in the conventional 10/20 system). The electrical potential was amplified with 0.1–100 Hz bandpass, digitized at 250 Hz sampling rate and stored on computer disk for the off-line analysis. The behavior of all participants was initially coded from the videotape so that only those trials in which the infants were fixating the center of the screen at target onset, without blinking, eye or head movements were included in the analysis of electrophysiological signals. Data from each sensor were removed if they contained artifacts created by movement or poor contact. The entire trial was excluded if data from more than 12 sensors had been removed or if the trial contained an eyeblink or other artifact. Missing data for infants with 10 or fewer bad channels were interpolated using spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989) from the individual participant averages. Data were baseline-corrected and then individual participant averages were computed for each trial type. Infants with less than 10 artifact-free trials in any condition were excluded. Individuals with more than 10 bad channels in their averages were also excluded from further analysis. The average number of trials making up these individual averages for Experiment 1 was 13.5 in the condition averted gaze/head to the right ($SD = 6.0$; range 5–26), 14.0 in the condition direct gaze/head to the right ($SD = 6.4$; range 3–27), 14.5 in the condition averted gaze/head to the left ($SD = 6.4$; range 8–27), and 13.9 in the condition direct gaze/head to the left ($SD = 6.4$; range 8–26); and was 24.3 in the direct gaze condition ($SD = 10.6$; range 11–40) and 22.3 in the averted gaze condition ($SD = 9.10$; range 11–38) for Experiment 2. Average ERPs were obtained time-locked to the presentation of faces with direct and averted gaze, oriented left and right (4 ERPs, Experiment 1), or inverted faces with direct and averted gaze (Experiment 2). ERP amplitudes

were baseline-corrected to the 100-msec prestimulus interval and were re-referenced to the average potential over the scalp (Lehmann, 1987). Scalp surface electrical maps were created by spherical interpolation (Perrin et al., 1989) and plotted in linear projection. ERP amplitude distribution was assessed by averaging the data within three lateral groups (left, medial, right) of four electrodes over the occipital cortex (see Figure 2). Whenever the Mauchly's test showed significant inhomogeneity of sphericity in the ANOVAs involving the laterality factor, we applied the Greenhouse–Geisser correction to assess significance.

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Note

1. The confound arises from the fact that pure condition effects can manifest themselves in condition by electrode interactions. If a component reflects the activation of a single source, and this activation affects the given electrode sites by different amounts, condition and electrode factors are not linearly additive as a general linear model would assume. The normalization procedure applied in our analysis can ensure that an interaction would not be falsely interpreted as reflecting activation of different sources in different conditions (for further details, see Picton et al., 2000).

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