Cortical Specialisation for Face Processing:

Face-sensitive Event-Related Potential components in 3 and 12 month old infants

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ABSTRACT

The adult N170 is considered to be an electrophysiological marker of specialised mechanisms for face processing. We investigated the development of cortical specialisation for face processing by characterising the developmental trajectory of the N170 over the first year of life. Experiment 1 sought to determine whether either of two face-sensitive infant ERP components (N290 and P400) previously identified in 6-month-olds (de Haan et al., 2002) correspond to the adult N170. Both the N290 and P400 increased in specificity for upright human faces compared to inverted human faces and monkey faces between 6 and 12-months of age. These findings indicate that the adult N170 is not preceded by a single developmental precursor, but rather emerges as a consequence of the integration of two functionally and morphologically distinct components (N290 and P400). Using the same procedure, Experiment 2 showed that the N290 and P400 in 3-month-olds are sensitive to the species of faces, but not their orientation. Since 6-month-olds show sensitivity to both, these results indicate that sensitivity to face orientation develops after sensitivity to the species of faces. The results of the two experiments indicate that face processing develops gradually over the first year of life in a manner that is consistent with an experience-dependent view of cortical specialisation.
INTRODUCTION
Evidence from single-cell recordings in monkeys, human neuropsychology, and functional neuroimaging converge to suggest that faces are processed by specialised neural and cognitive mechanisms that differ from those involved in the processing of other objects. For example, functional magnetic resonance imaging (fMRI) studies show that regions within the fusiform gyrus are more active when adults passively view faces than when they view other objects such as hands or chairs (Puce et al 1995; Puce et al 1996; Kanwisher et al 1997) and the pattern of activation over the ventral temporal cortex differs for faces compared to other objects (Ishai et al 1999). In addition, electrophysiological studies which measure scalp recorded brain electrical potentials (event-related potential, ERP) have consistently shown that faces elicit a negative potential that occurs most prominently over occipito-temporal scalp regions and peaks between 140-170ms after stimulus onset (Bentin et al 1996). This ERP component, the N170, is sensitive to faces in that it is of larger amplitude and shorter latency to faces compared with most other stimuli, including hands, feet, trees, cars, letters or words (Botzel and Grusser 1989; Botzel et al 1989; Bentin et al 1996; George et al 1996). Moreover, the amplitude and/or latency of the N170 also differs between upright human faces and closely related stimuli such as monkey or ape faces and inverted human faces (Eimer 2000c; Rebai et al 2001; Carmel and Bentin 2002; de Haan et al 2002). Whilst the functional significance of the N170 in adult face processing has yet to be fully elucidated, it is thought to reflect processing related to the structural encoding of faces as opposed to face recognition or face identification (Eimer 2000a; Eimer 2000b). This conclusion is based on findings demonstrating that the N170 is unaffected by the familiarity of faces but is sensitive to experimental
manipulations that alter the basic structural properties of faces e.g., inversion, feature scrambling (George et al 1996; Eimer 2000a; Eimer 2000b).

Despite previous efforts to establish the nature and degree of cortical specialisation for face processing, there is still considerable debate regarding how differences between face and object processing originate. There are currently several viewpoints that differ from each other in two main ways (reviewed in de Haan and Halit, 2001): (1) the degree to which cortical specialisation for face processing is determined by genetic or environmental factors and (2) the specificity of cortical processing mechanisms for faces only. According to one account, the neural mechanisms underlying face processing are genetically determined and are specific to faces (Farah 2000; Farah et al 2000). In this view, visual exposure to faces plays a minimal role in establishing the neural mechanisms underlying face processing, since a cortical module specifically dedicated to the processing of faces processing exists from birth. Evidence to support this view comes from a case study of a patient (Adam) who, as a result of a viral infection, suffered brain damage at only 1 day old. Tests carried out when he was 16 years of age revealed a disproportionate impairment in face recognition compared to object recognition (Farah et al 2000). Farah et al (2000) interpret these results as evidence that the distinction between face and object recognition, and the anatomical localisation of face recognition, are “explicitly specified in the genome” (p. 122).

In contrast to this view, two alternative accounts emphasise the critical role of experience viewing faces. One such account argues that neural specialisation for faces arises during development due to processes that parallel perceptual skill learning in adults (Diamond and Carey 1986; Gauthier and Nelson 2001). According to this view, development of specialised mechanisms occurs as a result of experience in making
fine-grained discriminations between numerous visually similar category members, and is not unique to faces per se. The development of specialised mechanisms responsible for the processing of upright faces thus occurs over time as a result of our extensive exposure to a large number of individual faces. In this view, mechanisms that are involved in the processing of faces are no different to those involved in tasks that require visual expertise for discriminating other categories with complex, visually similar members. These domain-general learning mechanisms may appear to be specific to faces only because faces are a stimulus category for which humans consistently develop a high level of expertise. Evidence to support this view has been obtained from behavioral and neuroimaging studies showing that effects previously thought to be specific to faces can also be obtained with other categories for which participants show expertise (Gauthier et al 1999; Gauthier et al 2000; Tarr and Gauthier 2000; Rossion et al 2002).

A third perspective explains data on the development of face processing in terms of developmental mechanisms that generate increasingly specialised processing within cortical areas (de Schonen & Mathivet, 1989; Johnson 2000; Johnson 2001; Nelson 1993; Nelson 2001). From this perspective, early in development a given region of cortical tissue may be activated by a broad range of stimuli. However, over time the selectivity of the cortical tissue increases so that it responds to only certain kinds of stimuli e.g., human upright faces. Thus, in this view an initially general mechanism becomes domain-specific. One possibility is that this process occurs via mechanisms that are analogous to those responsible for cortical specialisation of speech (Nelson 1993; Nelson 2001). In the first months of life infants are able to discriminate between a broad range of speech sounds, but with increasing age and experience, the range of speech sounds that infants respond to narrows. For example,
6 month-old infants can discriminate speech sounds from both native and non-native languages, whereas 12 month-olds and adults can only discriminate speech sounds that are part of their native language (Kuhl et al 1992; Cheour et al 1998). In a similar way, the face processing system may develop from a broadly-tuned, non-specific, complex-figure recognition system to system tuned in to the type of faces seen in the natural environment i.e., upright human faces (Nelson 1993, 2001). This view is supported by a recent study showing a decrease in discrimination abilities for non-human faces with age: 6-month-olds can discriminate between individual monkeys and humans, while 9-month-old infants and adults tested with the same procedure discriminate only between members of their own species (Pascalis et al 2002).

One way to evaluate these hypotheses is to investigate whether face-specific cortical areas are present early in life. Ethical and practical difficulties prohibit the use of most neuroimaging methods with healthy human infants; however, ERPs are one method that is suitable for use with this population. Information regarding the existence and stimulus-specificity of face-sensitive ERP components early in life is useful for at least two reasons. Firstly, it can help place constraints on theories concerning the influence of experience in development of face processing and secondly it can provide an important tool for investigating developmental disorders of social information processing e.g., (Dawson et al 2002). The first study to investigate face-sensitive components during infancy showed that at 6-months of age a positive component peaking at 400 ms over occipital electrodes was of shorter latency for faces compared to objects (de Haan and Nelson, 1999). However, the results of this study are difficult to interpret because there was no adult comparison group and because some of the objects were toys that had schematic faces.
Only one study has used the same procedure to compare face-sensitive ERP components in infants (6 months) and adults (de Haan et al. 2002). In that study, the specificity of infant and adult ERP responses was determined by comparing their responses to upright and inverted faces and to human and monkey faces. Inverted faces were used because they are identical to upright faces in their basic psychophysical properties, but adults are less familiar with them, and are worse at recognising them (Yin 1969). Since inversion typically has less or no influence on recognition of other objects (Yin, 1969), the “inversion effect” is considered to be an index of specialisation for face processing. Monkey faces were used because they share the basic structure of human faces (e.g., two eyes, above a nose, above a mouth), but adults are less familiar with them and are also worse at recognising them (Pascalis and Bachevalier 1998; Pascalis et al. 1998; Pascalis et al. 1999; Pascalis et al. 2001). The adult N170 showed specificity to upright human faces in two ways: (1) it was of smaller amplitude and shorter latency for upright human faces compared with all other face conditions and (2) face-inversion increased the amplitude and latency for human faces only (de Haan et al. 2002). The results obtained with 6-month-olds were consistent with the de Haan and Nelson (1999) study and showed that faces elicited a P400 occurring over posterior electrodes. Like the adult N170, the P400 was influenced by inversion: it was of larger amplitude for upright faces compared to inverted faces. However, unlike the adult N170, this effect was not specific to human faces and also occurred for monkey faces. A negative component preceding the P400 was also observed over posterior regions and peaked at 290 milliseconds after stimulus onset (N290). Like the adult N170, the N290 showed sensitivity to the species of faces in that it differed in amplitude between monkey and human faces. In contrast to the adult N170, the N290 showed no sensitivity to the orientation of faces.
Thus, while the N290 and P400 are possible candidates for an “infant N170”, neither component exhibited the same degree of specificity for upright human faces observed at the adult N170 (de Haan et al 2002).

In summary, it remains uncertain which, if any, of the two candidate infant components corresponds to the adult N170. One purpose of this study was to address this question by examining whether either component goes on to show adult-like specificity in response at an older age. Thus, in Experiment 1 we recorded high-density ERPs in 12 month olds using the same stimuli as de Haan et al (2002). A second purpose of this study was to investigate whether any degree of face-sensitivity could be observed at a younger age than has previously been tested. Thus, in Experiment 2 we used the same procedure with 3-month-old infants.

**EXPERIMENT 1: INTRODUCTION**

As described above, the ERP responses of 6-month-old infants do not share the same degree of specificity to upright human faces as the adult N170 (de Haan et al 2002). Whilst the adult N170 shows sensitivity to both the species and orientation of faces, an equivalent component has not yet been identified within the infant ERP. Instead, the effects of species and orientation occur at two separate time points within 6-month-olds ERP. Experiment 1 investigated whether either of the two infant components (N290 or P400) can be considered as developmental precursors of the adult N170 by examining the electrophysiological responses of 12-month-old infants while they passively viewed upright and inverted human and upright and inverted monkey faces. There are several possible outcomes for the N290 and P400: (1) neither component is a precursor to the adult N170, (2) only one of the two components is a
precursor, and (3) both components are precursors that are later integrated into a single N170 component.

Based on a prior behavioural study showing that infants “tune in” to human faces between 6-9 months (Pascalis et al. 2002), we predicted that at 12 months of age the specificity of the infant ERP to upright human faces would be more adult-like. Thus we aimed to identify the ERP component that most likely corresponds to the adult N170 by determining which component showed (a) sensitivity to both the species and orientation of faces, and (b) an inversion effect that is specific human faces. In other words, we predicted that, like adults, 12-month-olds would show an orientation by species interaction. On this basis we predicted that the amplitude and/or latency of the precursor to the adult N170 would differ between human faces and monkey faces and that inversion would increase the amplitude and/or latency of this component for human faces only.

**EXPERIMENT 1: METHODS**

**Participants**

The final sample consisted of 26 12-month-old infants (11 males) with an average age of 12 months (range=11:2-12:2 months). All were born full-term and were of normal birthweight. An additional 59 infants were tested but were excluded from further analysis due to eye and/or body movements that resulted in recording artefacts (n=58) or due to a procedural error (n=1).

**Stimuli**

The stimuli were 20 colour images of human female faces and 20 colour images of macaque monkey faces. The faces subtended a horizontal angle of 11° and a vertical
angle of 16° when viewed from a distance of 60cm and were presented against a grey background.

**ERP Recording**

ERPs were recorded using a Geodesic sensor net consisting of 63 silver-silver chloride electrodes evenly distributed across the scalp (Tucker 1993). A ground electrode was positioned at the back of the head above the neck. All bioelectrical signals were recorded using EGI NetAmps (Eugene, OR). The signals were recorded referenced to the vertex, with a bandpass filter of 0.1 – 100Hz and with gain set to 10,000 times. EEG was recorded continuously throughout the test sessions with a sampling rate of 250Hz. Stimulus duration was 1000ms with a variable interstimulus interval between 1000-3000 ms. The electro-oculogram was recorded from electrodes positioned above both eyes and on the outer canthi.

**Procedure**

After the sensor net was applied, each infant passively viewed the faces while seated on the carer’s lap in a dimly lit booth, approximately 60cms from a 21 inch-computer monitor mounted in a black background. Both infant and carer were readily observable to the experimenter at all times via a video camera situated on a wall above and behind the monitor. In order to gain a sufficient number of trials a partial between-participants design was used. Each infant was exposed to only two trial types: Half of the infants (n=13) viewed upright and inverted human faces, and the other half of infants viewed upright and inverted monkey faces. The two orientations were presented with equal probability and the order of presentation was random with the constraints that 1) each unique image in the set was shown before any was
repeated and 2) the same orientation was not repeated more than three times in succession. The maximum number of trials in the test session was 160, during which each of the 20 faces was presented four times for each orientation. Infants continued to view the stimuli until they became too fussy or bored to attend. Between trials the experimenter could activate a noise via a speaker located out of site beneath the presentation monitor and/or presented coloured patterns on the monitor to re-orient the infant’s attention to the screen if required. The average number of trials viewed for human faces was 142 and for monkey faces was 138.

**ERP Waveform Analysis**

The continuous EEG recording was divided to create segments from 100 ms pre-stimulus onset to 900 ms post-stimulus onset (i.e., 1000 ms segments). Data were digitally filtered offline with a 30Hz low-pass elliptical filter and then edited for artifacts. 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 10 sensors were excluded or if the trial contained an eye-blink. Data were baseline-corrected and then individual subject averages were computed for each trial type (Mean= 38 trials per condition). Individuals with greater than 6 bad channels in their averages were excluded from further analysis. Missing data for infants with 6 or fewer bad channels were interpolated using spherical spline interpolation from the individual subject averages. Data were re-referenced to the average reference.

Two time windows were chosen to capture the face-sensitive components identified in previous infant studies: (a) N290 (140 – 380ms) and (b) P400 (380-584 ms). The effects of orientation on the amplitude and latency of each component were tested by computing two measures: 1) Peak Amplitude (µV) within the target time
window, and 2) Peak Latency (ms) by calculating the time at which the peak (i.e.,
most negative or most positive depending on the polarity) occurred. These measures
were analysed in a 2x2x2x3 mixed ANOVA with SPECIES (human, monkey) as a
between subject factor, and ORIENTATION (upright/inverted), HEMISPHERE
(left/right) and CHANNEL group (Medial, Semi-Medial and Lateral) as within
subject factors. Further analyses were carried out when necessary using Sheffe’s test
or planned contrasts. Sensors that made up the channel groups were: Right Medial
(40,41), Left Medial (29,33), Right SemiMedial (44,45), Left SemiMedial (28,32),
Right Lateral (47, 48, 50), Left Lateral (26,27,31). For scalp distribution of sensors
see (Johnson et al 2001).

EXPERIMENT 1: RESULTS
Both human and monkey faces elicited a negative component that peaked
approximately 290 ms after stimulus onset (N290), which was followed by a positive
component that peaked at 400ms (P400) after stimulus onset. The amplitude and
latency of both ERP components were analysed to test for effects of species and
orientation. Figure 1 shows the grand-averaged waveforms from two posterior
temporal recording sites for upright and inverted human faces and upright and
inverted monkey faces. Means and standard deviations of peak amplitudes and
latencies of the N290 and P400 are shown in Tables 1 and 2.

N290
The general characteristics of the N290 showed that it was of longer latency at
Lateral compared with SemiMedial and Medial sensors for both monkey and human
faces (Main effect of CHANNEL, F(2,48)=5.47 P<0.01, Post-hoc: Lateral – Medial,
F(1,24)= 6.20 P=0.02, Lateral-SemiMedial, F(1,24)=9.30 P<0.01) and increased in amplitude from Lateral to SemiMedial to Medial sensors (Main effect of CHANNEL, F(2,48)=22.51 P<0.001, Post-hocs: Lateral – Medial, F(1,24)=27.07 P<0.001; Lateral – SemiMedial, F(1,24)=23.99 P<0.001; Medial – SemiMedial, F(1,24)=12.97 P<0.001). The N290 was also larger over the left compared with the right hemisphere at SemiMedial sensors only (HEMISPHERE x CHANNEL interaction, F(2,48)=4.46 P<0.02; Post-hoc: SemiMedial: Left – Right, F(1,24)=3.91 P<0.05).

The N290 showed sensitivity to the species of faces in that it was of longer latency for human compared to monkey faces (Main effect of SPECIES, F(1,24)=16.00 P<0.005) and was of larger amplitude for human compared with monkey faces (Main effect of SPECIES, F(1,24)=15.57 P<0.01). The effect of Species on the amplitude of the N290 was most prominent over Medial and SemiMedial sensors (SPECIES x CHANNEL interaction, F(2,48)=10.50 P<0.001; Post – hoc: Medial: human-monkey, F(1,24)= 24.97 P<0.001; SemiMedial: human-monkey, F(1,24)=9.10 P<0.001). The N290 showed sensitivity to the orientation of faces in that it was larger for inverted compared with upright human faces, but did not differ for inverted compared to upright monkey faces (SPECIES x ORIENTATION interaction, F(1,24)=4.57 P<0.05; Post-hocs: Upright – Inverted human faces, F(1,24) =7.21 P<0.02).

**P400**

The general characteristics of the P400 showed that it was of longer latency at SemiMedial and Medial than at Lateral sensors (Main effect of CHANNEL, F(2,48)=10.77 P=<0.001; Post – hocs: Lateral – Medial, F(1,24)=14.87 P<0.001, Lateral – SemiMedial, F(1,24)= 22.06 P<0.001) and was of larger amplitude at Lateral
compared with Semi-Medial or Medial sensors (Main effect of CHANNEL, F(2,48)=11.49 P<0.001; Post-hocs: Lateral – Medial, F(1,24)=13.01 P<0.001, Lateral – SemiMedial, F(1,24)=33.21 P<0.001. The main effect of CHANNEL on P400 amplitude was modified by a HEMISPHERE x CHANNEL interaction (F(2,48)=3.42 P<0.05), which occurred because there was a trend for P400 amplitude was larger over the right than the left hemisphere at lateral sensors only (F(1,24)=3.52 P<0.1).

The P400 showed sensitivity to the species of faces in that it peaked more quickly for human faces compared with monkey faces (Main effect of SPECIES, F(1,24)=11.28 P<0.01). However, there were no effects of SPECIES on the amplitude of the P400. In addition, the P400 showed sensitivity to the orientation of faces in that its latency was longer for inverted compared to upright faces at lateral sensors only (ORIENTATION x CHANNEL INTERACTION, F(2,48)=5.90 P<0.01; Post-hocs: Lateral Sensors: Upright – Inverted, F(1,24)=7.12 P<0.01). However, this pattern was only significant for human faces as shown by the three-way SPECIES x ORIENTATION x CHANNEL interaction (F(2,48)=5.90 P<0.01; Post – hoc: Human: Lateral – Upright/ Inverted, F(1,24)=16.10 P<0.001, with a similar trend at Human: SemiMedial – Upright/ Inverted, F(1,24)=3.38 P<0.1). There were no effects of Orientation on the amplitude of the P400.

**EXPERIMENT 1: DISCUSSION**

The purpose of Experiment 1 was to identify and characterise an ERP component in 12-month-olds whose response properties most closely resemble the adult N170. We focused on two ERP components (the N290 and P400) which at 6-months of age were found to be sensitive to either the species or orientation of faces, but not both. We aimed to see whether by 12 months of age either component would, like the adult
N170, show an interaction of species by orientation. The results showed that both components became more adult-like by this criterion. The amplitude of the N290 was larger for inverted than upright human faces, but not monkey faces; and, the latency of the P400 over lateral sensors was longer for inverted than upright human, but not monkey faces. Neither of these patterns of response were observed at 6 month of age, but both are characteristics of the adult N170 (de Haan et al., 2002). Overall, these data demonstrate an increase in the specificity of cortical responses with age. Since the response properties of both the N290 and P400 show an increased specificity to human faces with age, neither can be ruled out as a precursor to the adult N170.

While the functional specificity of infants’ ERPs becomes more adult-like between 6 and 12 months of age, differences between the characteristics of infant and adult ERPs remain. For example, the latency of infant ERPs is delayed relative to the adult N170. The delayed latency of infant ERPs is consistent with previous studies which found that the latency of the N170 in response to faces decreases between 4 and 14 years of age and adulthood (Taylor et al 1999; Taylor et al 2001). A decrease in the latency of ERP components with age does not appear to be specific to faces or visual ERPs since it has also been demonstrated for auditory ERPs elicited by harmonic tones (Kushnerenko et al 2002) and has been attributed to factors typically involved in brain maturational processes e.g., increased synaptic density, advanced myelination, efficacy, and synchronisation (Vaughan and Kurtzberg 1992). Secondly, the scalp distribution of infant ERPs is medial, whereas the adult N170 is most prominent at lateral recording sites. This difference could be due to physical differences (e.g., skull thickness) between infants and adults and/or due to differences in the configuration of generator(s) underlying the infant and adult components (see de Haan et al., 2002 for further discussion).
EXPERIMENT 2: INTRODUCTION

The aim of Experiment 2 was to investigate the development of cortical specialisation for faces by examining the functional characteristics of the N290 and P400 in 3-month-olds. As in Experiment 1, infants passively viewed images of upright and inverted human faces and upright and inverted monkey faces. Since 3-month-olds have had even less experience of faces than 6-month-olds we hypothesised that their ERP components would either exhibit the same or less specificity for human faces than 6-month-olds (de Haan et al 2002). Therefore the predictions for the N290 were (1) Like 6-month-olds, its amplitude would not differ between upright and inverted human or monkey faces (2) Like 6-month-olds, it may show sensitivity to the species of a face and this would be seen as an increased amplitude to human faces compared with monkey faces. The predictions for the P400 were (1) it may show sensitivity to the species of faces in that it would peak more quickly for human faces compared with monkey faces (2) it may be sensitive to the orientation of faces but the effects would not be specific to human faces.

EXPERIMENT 2: METHODS

The stimuli, general methods for data collection and data analysis as well as statistical analysis were the same as in Experiment 1. The only difference being the two time windows that were chosen to capture the face-sensitive components. These were: (a) N290 (120-440) and (b) P400 (440-690). The time windows differed from those
selected for the 3-month-olds because as predicted their ERP components occurred at
a later time point within the ERP waveform than those observed in 12-month-olds
(Experiment 1) and 6-month-olds (de Haan et al., 2002).

Participants
The final sample consisted of 25 3-month-old infants (13 males) with an average age
of 3-months (range=2:3-3:1 months). All were born full-term and were of normal birth
weight. An additional 43 infants were tested but were excluded from further analysis
due to eye and/or body movements that resulted in recording artefacts (n=13) or
because of general fussing during the recording so that too few trials could be
obtained (n=30).

Results
Both human and monkey faces elicited a negative component that peaked
approximately 350ms after stimulus onset, which was followed by a positive
component that peaked maximally at 480ms after stimulus onset. The amplitude and
latency of both ERP components were analysed to test for effects for species and
orientation. Figure 2 shows the grand-averaged waveforms from two posterior
temporal sites for upright and inverted human faces and upright and inverted monkey
faces. Means and standard deviations for peak amplitudes and latencies of the N290
and P400 are given in Tables 3 and 4.

N290
The general characteristics of the N290 showed that it was of largest amplitude (i.e.,
most negative) at Medial sensors for both monkey and human faces (Main effect of
CHANNEL, F(2,46)=5.53  P<0.01; Post-hoc: Lateral versus Medial sensors:
F(1,23)=6.08 P=0.02; Medial- Semi-Medial, F(1,23)=12.78 P<0.01). No main effect of latency was found for the N290.

No main effect of species was found for the amplitude of the N290, but a three-way interaction (SPECIES x HEMISPHERE x CHANNEL) showed that compared with monkey faces, human faces elicited a larger N290 in the right hemisphere and at Medial sensors only (SPECIES x HEMISPHERE x CHANNEL Interaction, F(2, 46)=7.43 P<0.01; Post-hoc: Monkey versus Human at Right Medial sensors only: F(1,23)<0.05 (One-tailed). The N290 was longer in latency to monkey faces compared with human faces (Main effect of SPECIES, F(1,23)=9.70 P<0.01). In addition, a three-way interaction (SPECIES x HEMISPHERE x CHANNEL) showed that there were no latency differences at the N290 for monkey faces in both the left and right hemisphere, however, the N290 elicited by human faces was shorter in latency in the right hemisphere compared with the left hemisphere at lateral sensors only (SPECIES x HEMISPHERE x CHANNEL Interaction: F(1,23)=18.46 P<0.001; Post-hoc: Human faces: Right versus Left Hemisphere at Lateral sensors only F(1,23)=18.46 P<0.001. No significant effects of orientation were found for both the amplitude and latency of the N290.

**P400**

The general characteristics of the P400 showed that its amplitude was largest (i.e., most positive) at Semi-Medial sensors for both human and monkey faces (Main effect of CHANNEL, F(2,46)=6.96 P<0.01; Post-hoc: Medial versus SemiMedial sensors: F(1,23)=24.75 P<0.001. In addition, the P400 peaked most quickly at Semi-Medial sensors (Main effect of CHANNEL, F(2,46)=6.12 P<0.01; Post-hoc: Medial versus SemiMedial sensors: F(1,23)=11.88 P<0.01. The latency of the P400 was found to
peak more quickly for human faces compared with monkey faces (Main effect of SPECIES, F(1,23)=13.48 P<0.01), and no main effect of species was found for the amplitude of the P400. A three-way interaction (SPECIES x HEMISPHERE x CHANNEL) showed that the amplitude of the P400 was larger in the right hemisphere for human faces compared with monkey faces at lateral sensors only (SPECIES x HEMISPHERE x CHANNEL Interaction, F(2,46)=10.03 P<0.001; Post-hoc: Human faces versus Monkey Faces in Right Hemisphere at Lateral sensors only F(1,23)=6.84 P<0.02). Although no main effects of orientation were found for both the amplitude and latency of the P400 a two-way interaction (SPECIES x CONDITION) showed that inverted monkey faces elicited the smallest P400 amplitude compared with all other face conditions which did not significantly differ from each other (SPECIES x ORIENTATION Interaction: F(1,23)=6.27 P<0.02; Post hoc: F(1,23)=8.17 P<0.01). A three-way interaction (SPECIES x CONDITION x CHANNEL) showed that the latency of the P400 peaked more quickly for inverted human faces compared with upright faces in the right hemisphere only (SPECIES x CONDITION x CHANNEL Interaction: F(1,23)=5.74 P=0.03, Post-hoc: Upright Human versus Inverted Human in Right Hemisphere only: F(1,23)=8.35 P<0.01).

EXPERIMENT 2: DISCUSSION

The aim of experiment 2 was to investigate the development of cortical specialisation for faces by examining the functional characteristics of the N290 and P400 in 3-month-olds. The N290 peaked at around 350ms after stimulus onset and was most prominent at medial recording sites. The delayed latency of the N290 and its medial scalp distribution are consistent with results obtained in 12-month-olds (Experiment 1). The N290 showed sensitivity to the species of a face in that it was of
larger amplitude and shorter latency for human faces compared with monkey faces in
the right hemisphere only. As predicted, at 3 months of age the N290 did not show
sensitivity to the orientation of human or monkey faces. These findings show that the
degree of specificity found at the N290 for upright human faces is similar to that
observed at 6-months of age (de Haan et al 2002), but less than that observed in 12-
month-olds and adults.

The effects of inversion and species were also examined at the P400. The
P400 peaked at 480ms after stimulus onset and was of shorter latency for human faces
compared with monkey faces. This finding is consistent with the P400 recorded in 12-
month-olds and suggests that at both ages infants process human faces more quickly
than monkey faces. The amplitude of the P400 was larger in the right hemisphere for
human faces compared with monkey faces at lateral sensors only. In contrast to 6-
month-olds, the P400 in 3-month-olds was not affected by orientation. The N290 and
P400 responses to the species and orientation of faces show that 3-month-olds are
sensitive to the species of faces but are not sensitive to orientation of faces. Together
with the 6-month-old findings, these data suggest that sensitivity to face orientation
develops later than sensitivity to the species of faces.

**GENERAL DISCUSSION**

The general aim of the present study was to use ERPs to investigate the development
of cortical specialisation for face processing by characterising the developmental
trajectory of the N170 over the first year of life. Experiment 1 aimed to investigate
whether either of two ERP components (N290 and P400) previously identified in 6-
month-olds (de Haan et al 2002) correspond to the adult N170. The specificity of 12-
month-old infants ERP responses to faces was examined using upright and inverted
human faces or upright and inverted monkey faces. The results showed that both the species and orientation of faces affected either the amplitude or latency of the N290 and P400. In contrast, at 6 months of age the N290 shows sensitivity the species of faces but not to the orientation of faces and the P400 shows sensitivity to the orientation of faces but not the species of faces. At 12-months of age, the N290 showed specificity to human faces in several ways: (1) its amplitude and latency differed between human and monkey faces, and (2) an inversion effect occurred for human faces only. The P400 showed specificity for human faces in two ways (1) it peaked more quickly for human faces compared to monkey faces and (2) it was of longer latency for inverted compared to upright human faces. These findings show that the specificity of the N290 and the P400 increases between 6 and 12 months of age: both become more specific to upright human faces.

On the basis of functional properties alone, our results suggest that neither the N290 nor P400 can be ruled out as developmental precursors of the adult N170. In terms of component timing and polarity, the N290, as opposed to the P400, is more similar to the adult N170, and on this basis has previously been labelled as the “infant N170” (de Haan et al., 2002). According to similar criteria, the P400 might be interpreted as the infant equivalent of the adult P2 which follows the N170. However, since the adult P2 is not influenced by inversion or species the findings are more consistent with the view that the P400 reflects functions that are linked to the adult N170. One interpretation is that the P400 reflects processes that become integrated with the N290 to eventually produce the mature N170 (de Haan et al., 2002). In other words, part of the process of development of specialisation of face processing may involve integrating in time initially disparate or overlapping processing stages to an early stage of visual processing. In this view, processing that takes place at the P400
during infancy may occur more rapidly during adulthood reflecting increased specialisation for face processing.

Experiment 2 investigated the development of cortical specialisation by examining the response properties of the N290 and P400 in 3 month-olds. At 3 months the N290 showed sensitivity to the species of faces in that it was of larger amplitude and shorter latency for human faces compared with monkey faces, in the right hemisphere only. These findings are broadly consistent with those obtained in 12-month-olds (Experiment 1) and 6-month-olds (de Haan et al. 2002), which showed that the N290 (bilaterally) was larger in amplitude to human faces compared with monkey faces. At 3 months of age the N290 did not show sensitivity to the orientation of human or monkey faces. This finding is consistent with data obtained at 6 months of age which demonstrated that the N290 did not differ between upright or inverted human or monkey faces (de Haan et al. 2002). In contrast, at 12-months of age the N290, like the adult N170, was more negative in amplitude to inverted human faces compared with upright human faces, but was of equal amplitude for upright and inverted monkey faces. Together, these data suggest that at 3 and 6 months of age the response properties of the N290 are similar to each other but differ to the N290 in 12-month-olds and the adult N170.

At 3 months of age the latency of the P400 was shorter for human faces compared with monkey faces. The latency of the P400 was also shorter for human faces at 12-months of age, suggesting that at both ages infants process human faces more quickly than monkey faces. At 6 months of age the P400 shows no latency differences between human and monkey faces (de Haan et al. 2002), although it is of shorter latency for objects compared to human faces (de Haan and Nelson 1999). At 3 months of age the P400 did not differ between upright and inverted faces, whereas at
6 and 12 months of age, orientation dependent amplitude and latency changes were observed at the P400. These results suggested that sensitivity to orientation of faces develops sometime between 3 and 6 months, and that it develops after sensitivity to the species of a face.

When viewed in terms of cortical specialisation, the functional characteristics of the N290 and P400 at 3 months of age suggests that their cortical responses to faces are less specialised than those observed in older infants and adults. This general pattern of results is consistent with the view that experience with faces plays a role in the development of specialised cortical mechanisms responsible for processing faces. In particular, the emergence of an adult-like inversion effect between 6 and 12 months is consistent with results from a recent study which showed that visual experience with individual exemplars of a category can lead to the emergence of similar effects of face-inversion at the N170 (Rossion et al 2002). At present it is unclear whether the acquisition of expertise in later life is the same or different from acquiring expertise during development. Investigating the parallels between adult learning and infant development would help elucidate the role of the infant N290 and P400 in face processing. If it is the case that the functions of the N290 and P400 become integrated during adulthood to produce the adult N170 then it would be interesting to know (a) at what age this occurs and (2) whether in early stages of adults’ perceptual learning, P2 effects are observed which are later integrated into the adult N170.

In summary, the increased specificity of the N290 and P400 for upright human faces between 3 and 12-months of age suggests that cortical specialisation develops in a gradual manner, and is not fully mature even at the end of the first year of life. Moreover, our results indicate that the adult N170 is not preceded by a single
precursor but rather emerges as a consequence of an integration between two functionally and morphologically distinct components, namely the N290 and P400.
ACKNOWLEDGMENTS

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REFERENCES


**Figure 1.** Grand-averaged waveforms obtained for upright and inverted human faces (top) and upright and inverted monkey faces (bottom), at left (channel 32) and right (channel 44) posterior temporal recording sites at 12 months of age.
Figure 2. Grand-averaged waveforms obtained for upright and inverted human faces (above) and upright and inverted monkey faces (below), at left (channel 32) and right (channel 44) posterior recording sites at 3 months of age.
### TABLE 1: Mean Amplitude and Mean Latency of N290 for 12-month-olds

<table>
<thead>
<tr>
<th>N290</th>
<th>Human</th>
<th>Monkey</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>AMPLITUDE</strong></td>
<td>Upright</td>
<td>Inverted</td>
</tr>
<tr>
<td><strong>Left</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lateral</td>
<td>-8.3 (6.4)</td>
<td>-13.4 (7.4)</td>
</tr>
<tr>
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<td>-8.7 (8.0)</td>
<td>-12.8 (10.6)</td>
</tr>
<tr>
<td>Medial</td>
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<td>-8.2 (7.3)</td>
</tr>
<tr>
<td><strong>Right</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lateral</td>
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<td>-11.7 (10.2)</td>
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<tr>
<td>Medial</td>
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<td>-9.6 (11.5)</td>
</tr>
<tr>
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<td></td>
</tr>
<tr>
<td><strong>Left</strong></td>
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<td></td>
</tr>
<tr>
<td>Lateral</td>
<td>315 (51)</td>
<td>317 (48)</td>
</tr>
<tr>
<td>Semi-Medial</td>
<td>292 (44)</td>
<td>310 (29)</td>
</tr>
<tr>
<td>Medial</td>
<td>295 (24)</td>
<td>283 (31)</td>
</tr>
<tr>
<td><strong>Right</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lateral</td>
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<td>301 (34)</td>
</tr>
<tr>
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<tr>
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### TABLE 2: Mean Amplitude and Mean Latency of P400 for 12-month-olds

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<td>Inverted</td>
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<td><strong>Left</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lateral</td>
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<td>Lateral</td>
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<td></td>
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<tr>
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<td>Medial</td>
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<td>392 (21)</td>
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Table 3: Mean Amplitude and Mean Latency of N290 for 3-month-olds

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<th>Monkey</th>
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<td>Left</td>
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Table 4: Mean Amplitude and Mean Latency of P400 for 3-month-olds

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<td>6.4 (4.4)</td>
<td>4.9 (4.2)</td>
<td>3.4 (2.5)</td>
</tr>
<tr>
<td>Right</td>
<td>Lateral</td>
<td>8.7 (4.9)</td>
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<td>5.0 (4.4)</td>
<td>3.5 (3.2)</td>
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<td></td>
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