Specialization of Neural Mechanisms Underlying Face Recognition in Human Infants

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Abstract

■ Newborn infants respond preferentially to simple face-like patterns, raising the possibility that the face-specific regions identified in the adult cortex are functioning from birth. We sought to evaluate this hypothesis by characterizing the specificity of infants' electrocortical responses to faces in two ways: (1) comparing responses to faces of humans with those to faces of nonhuman primates; and 2) comparing responses to upright and inverted faces. Adults' face-responsive N170 event-related potential (ERP) component showed specificity to upright human faces that was not observable at any point in the ERPs of infants. A putative "infant N170" did show sensitivity to the species of the face, but the orientation of the face did not influence processing until a later stage. These findings suggest a process of gradual specialization of cortical face processing systems during postnatal development. ■

INTRODUCTION

Faces are highly salient and biologically significant visual stimuli that provide information critical for successful negotiation of the social world, such as the identity, age, and emotional state of those around us. Adults are expert in perceiving this information: They are typically able to recognize faces more quickly and more accurately than other types of visual stimuli (Yin, 1969) and can remember large numbers of individual faces over long periods (Bahrick, Bahrick, & Wittilinger, 1975). The reason for this expertise is at the center of current debate: Does it reflect the existence of specialized neural mechanisms devoted exclusively to face processing, or does it reflect a type of acquired visual expertise that, except for being very consistently acquired across individuals, is no different from expertise that can be acquired for other categories of complex visual stimuli?

The hypothesis that there are neural mechanisms uniquely devoted to face processing was first proposed by Bodamer (1947) who noted that some patients are more impaired in face than object processing following damage to the brain. More recently, this hypothesis has been investigated using neuroimaging and neurophysiological techniques. These studies indicate that in human adults, particular areas of ventral and lateral occipital cortex are preferentially activated by faces (Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995; Puce, Allison, Asgari, Gore, & McCarthy, 1996) and that face processing is impaired if they are damaged (Damasio, Tranel, & Damasio, 1990) or experimentally stimulated (Allison, McCarthy, Nobre, Puce, & Belger, 1994). While these areas are often described as discrete modules, there is evidence for a more continuous representation of visual form information (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999).

Activity of one or more of these areas likely underlies the N170, a face-sensitive brain electrical potential (event-related potential, ERP) recorded from the scalp surface using electroencephalography (Bentin, Allison, Puce, Perez, & McCarthy, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996). The N170 is a negative deflection that is most prominent over occipito-temporal scalp and peaks between 140 and 170 msec after stimulus onset. It is sensitive to faces in that its latency is shorter and amplitude larger for upright faces compared to many other stimuli such as hands, feet, trees, cars, buildings, letters, or words (Bentin et al., 1996; George et al., 1996; Carrieté & Iglesias, 1995; Botzel & Grusser, 1989, Botzel, Grusser, Haussler, & Naumann, 1989). The N170 elicited by the full face is, however, smaller than that elicited by the eyes alone (Cauquil, Edmonds, & Taylor, 2000; Bentin et al., 1996), a finding suggesting that the N170 may primarily reflect the processing of the eyes. However, the observations that faces with and without eyes elicit N170s of the same amplitude (Eimer, 1998) and that larger-amplitude and slower-latency N170s are also elicited by inverted or scrambled faces (with eyes present) than upright faces, argue against this view (Rossion et al., 2000b; Eimer & McCarthy, 1999). The N170 may instead be linked to "... late stages of structural encoding, where representations of global

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face configurations are generated in order to be utilized by subsequent face recognition processes'' (Eimer, 2000).

While the evidence reviewed above might seem to support the existence of a neural system dedicated to processing human faces, several recent reports question this conclusion. For example, the same fusiform areas that are preferentially activated by faces can also be preferentially activated by other categories with which the perceiver has extensive experience. The ''face responsive'' area is activated by cars in car experts and by birds in bird experts (Gauthier, Skudlarski, Gore, & Anderson, 2000). This suggests that visual experience in discriminating individual members of a particular category plays an important role in forming category-sensitive cortical responses. One hypothesis is that the development of expertise in face processing is no different from the development of expertise in recognizing individual members of other categories of complex visual stimuli. It may only be that faces are one of the only, or the only, category, for which this ability develops consistently across the human population. However, studies of adults cannot fully test this hypothesis because they examine the system only in its end ''expert'' state. Merely showing that visual expertise can be acquired for nonface categories later in life does not necessarily prove that visual expertise for face processing developed in the same way. An alternative possibility remains that there are innate mechanisms devoted specifically to face processing but that these areas can later be recruited for processing in other situations that pose similar processing demands (e.g., requiring memory for multiple highly similar exemplars within a complex visual category). Because infants begin to learn about faces from very early in life, the role of expertise in the development of face recognition can only be investigated fully by studying the face processing system as it develops.

Studies of face recognition in young infants show that newborn infants respond preferentially to certain simple face-like patterns (Valenza, Simion, Cassia, & Umilta, 1996; Johnson, Dziurawiec, Ellis, & Morton, 1991; Goren, Sarty, & Wu, 1975), raising the possibility that the face-specific region of the cortex observed in adults is active from birth. However, an alternative view is that the tendency of the newborn to orient to faces is largely mediated by subcortical structures, and that there is subsequently an experience-dependent specialization of circuits in the ventral occipito-temporal pathway for processing faces (Johnson & Morton, 1991; de Schonen & Mathivet, 1989). This process of specialization might be seen as increases in the selectivity of response patterns of cortical tissue in response to a particular input. For example, a given region of cortical tissue may originally respond to a wide range of objects, but with experience, one may narrow the range to just one class, such as faces. If this is true, one would expect developmental changes in the specificity of cortical processing of faces over the first years of life.

The purpose of the present study was to examine the development of cortical specialization for face processing. Since functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) imaging methods cannot presently be used to study healthy human infants, we used ERPs to address this question by examining whether human infants, like adults, show cortical potentials selective for upright human faces. A prior study has shown that an N170 component that is of larger amplitude and shorter latency for faces than objects is observable in children as young as 4 years of age (Taylor, McCarthy, Saliba, & Degiovanni, 1999). The same study showed that the N170 undergoes developmental change involving a decrease in peak latency and an increase in peak amplitude with age. In view of this developmental trend, we expect that, if the N170 is present in infants, it will be of longer latency and smaller amplitude than in adults or children.

We examined the specificity of the response in two ways. First, we compared responses to human faces with responses to faces of another species, monkeys, whose faces have a similar configuration of features as human faces. We predicted that adults' N170s would be of larger amplitude and longer latency for monkey faces than for upright human faces. Our prediction is based on prior findings showing that manipulations of the face that disrupt configural encoding, such as inversion (Rossion et al., 2000b; Eimer & McCarthy, 1999), increase the amplitude and latency of the N170. We expected monkey faces to be similar to inverted human faces in this regard, since it is known that adults are worse in recognizing facial identity in both monkey faces and inverted human faces than in upright human faces (e.g., Pascalis & Bachevalier, 1998; Yin, 1969). fMRI studies with adults indicate that inverted human faces activate both face-sensitive regions of the cortex, such as the so-called fusiform face area (Kanwisher, Tong, & Nakayama, 1998), and additional adjacent areas of the cortex involved in object recognition (Haxby et al., 1999). Thus, in adults, stimuli that are recognizable as faces but are not upright human faces (e.g., monkey faces, inverted human faces) may engage both face-sensitive regions and additional object processing regions and thereby elicit a larger amplitude N170 than the upright human face.

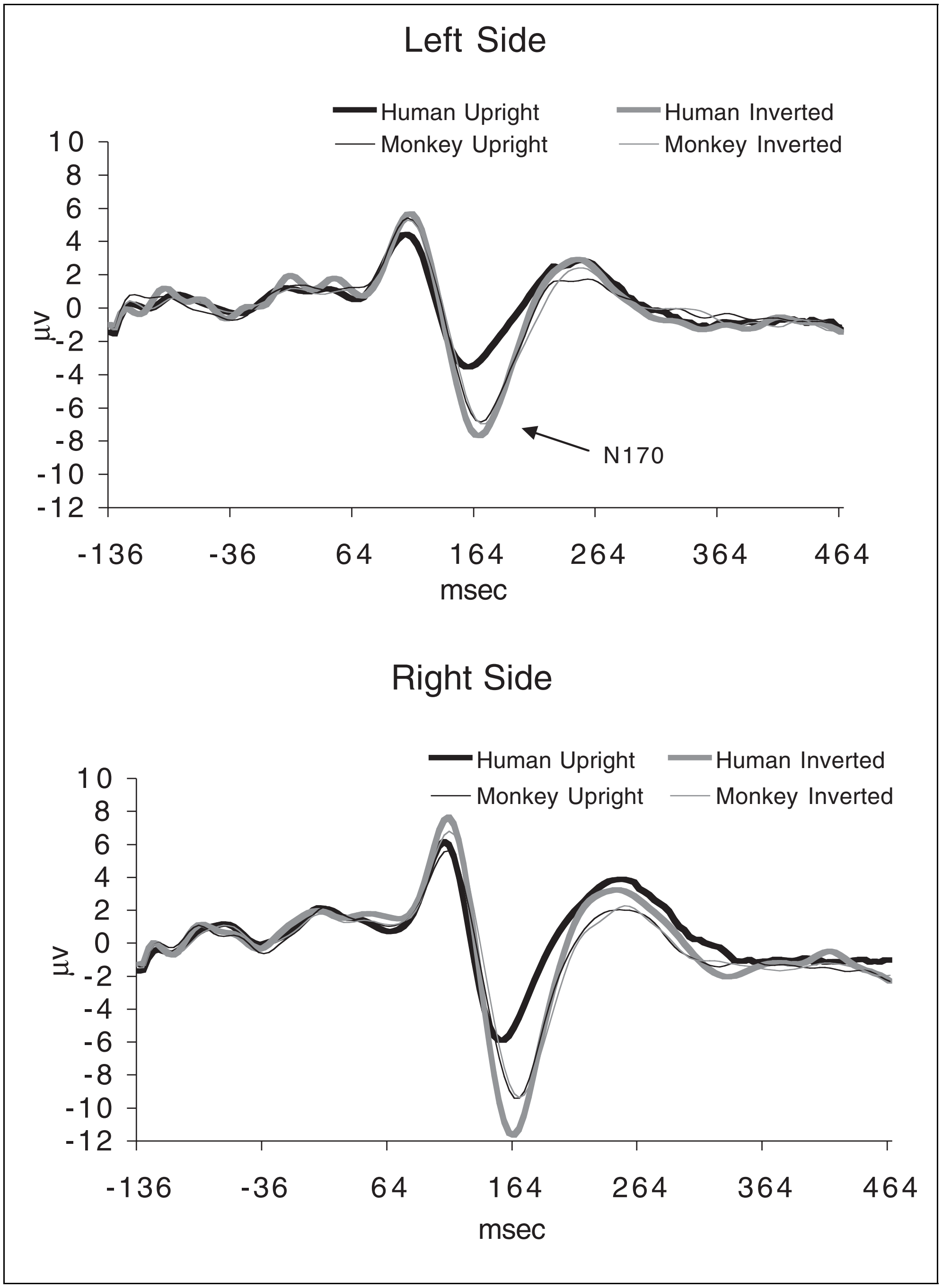
The second way we examined the specificity of the response was to compare the effects of inversion on responses to human faces and monkey faces. The susceptibility of face processing to the detrimental effects of stimulus inversion has been interpreted as a sign of adults' extensive experience and special expertise with upright faces (Rossion et al., 2000a). Previous studies have shown that inversion of human faces increases the amplitude and latency of the N170 and that similar inversion effects can be seen for other categories only with extensive training in discriminating and remembering examples from the category (Rossion et al., 2000a). Thus, we expected that, even though they share the same overall configuration, inversion would influence the N170 elicited by human faces but not monkey faces.

To summarize, we expected that the specialization of the adult face processing system would express itself in two ways: (a) the N170 would be of larger amplitude and longer latency for upright monkey than upright human faces; and (b) inversion would affect the N170 only for human faces. We hypothesized that, if there is an innately specialized cortical system for processing faces, a component with similar response properties would be observable in the infant ERP.

RESULTS

We recorded ERPs from a high-density array (129 electrodes) while adults (n = 11) passively viewed upright and inverted human and monkey faces. The waveforms from two posterior temporal electrodes (T5, T6) are displayed in Figure 1. All stimuli elicited an N170 component over occipito-temporal electrodes that de-

Figure 1. Grand average of adults' (n = 11) ERPs to upright human faces ━━, inverted human faces ━━, upright monkey faces ——, and inverted monkey faces —— at the right posterior temporal (T6) and left posterior temporal (T5) electrodes.



creased in amplitude from medial to lateral recording sites [Main effect of Electrode, $F(1,10) = 11.36$, $p < .01$]. The N170 differed in amplitude for upright human faces compared to all other stimuli. Difference contrasts computed for the four types of faces showed that the amplitude of the N170 elicited by upright human faces was smaller than that elicited by the other faces [$F(1,10) = 10.93$, $p < .01$]. In contrast, the amplitudes for inverted human faces, upright monkey faces, and inverted monkey faces did not differ significantly from one another ($p > .1$). The uniqueness of the response to human faces is illustrated in Figure 2 in the spline maps of the amplitude distributions at the peak of the N170: The maps for human inverted faces, monkey upright faces, and monkey inverted faces look most like one another and different from the map for human upright faces.

Further analyses showed that inversion affected only human faces: It increased the amplitude of the N170 for human faces but not for monkey faces [Species × Orientation interaction, $F(2,20) = 20.05$, $p < .01$], and it increased the latency of the N170 for human faces but not for monkey faces (Species × Orientation interaction, $F(1,10) = 8.31$, $p < .05$]. For human faces, the effects of inversion on N170 peak amplitude were greater over the right than the left side [Species × Orientation × Hemisphere interaction, $F(2,20) = 13.51$, $p < .01$] and over lateral compared to medial electrodes [Species × Orientation × Electrode interaction, $F(4,40) = 20.39$, $p < .01$].

The N170 also differed in latency for human compared to monkey faces: It peaked more quickly [Main effect of Species, $F(1,10) = 17.36$, $p < .01$] for human faces compared to monkey faces, regardless of the orientation of the face.

To summarize, the adult N170 showed specialization to upright human faces in two ways: The amplitude of the N170 was different for upright human faces compared to other stimuli (especially over right, lateral sensors), and inversion increased the amplitude and latency of the N170 only for human faces.

In order to determine whether this pattern of specificity was observable in the electrocortical response to faces very early in life, ERPs were recorded while 6-month-old infants passively viewed upright and inverted human ($n = 17$) or monkey ($n = 17$) faces. A partial between-subjects design was used in order that, even with infants' more limited attention spans, sufficient numbers of trials could be collected for each condition. The waveforms for infants are displayed in Figure 3.

We first analyzed a negative deflection occurring between 260 and 336 msec whose morphology appeared generally similar to the N170 (see Figure 3). This component was larger over medial than lateral sensors [Main effect of Electrode, $F(1,32) = 7.77$, $p < .01$]. There was a main effect of Species, [$F(1,32) = 7.64$, $p < .01$] on the amplitude of this component: The negativity was larger for human (−2.19 μV) than for monkey ($M = 4.12$ μV) faces. This Species effect was largest over medial electrodes [Species × Electrode

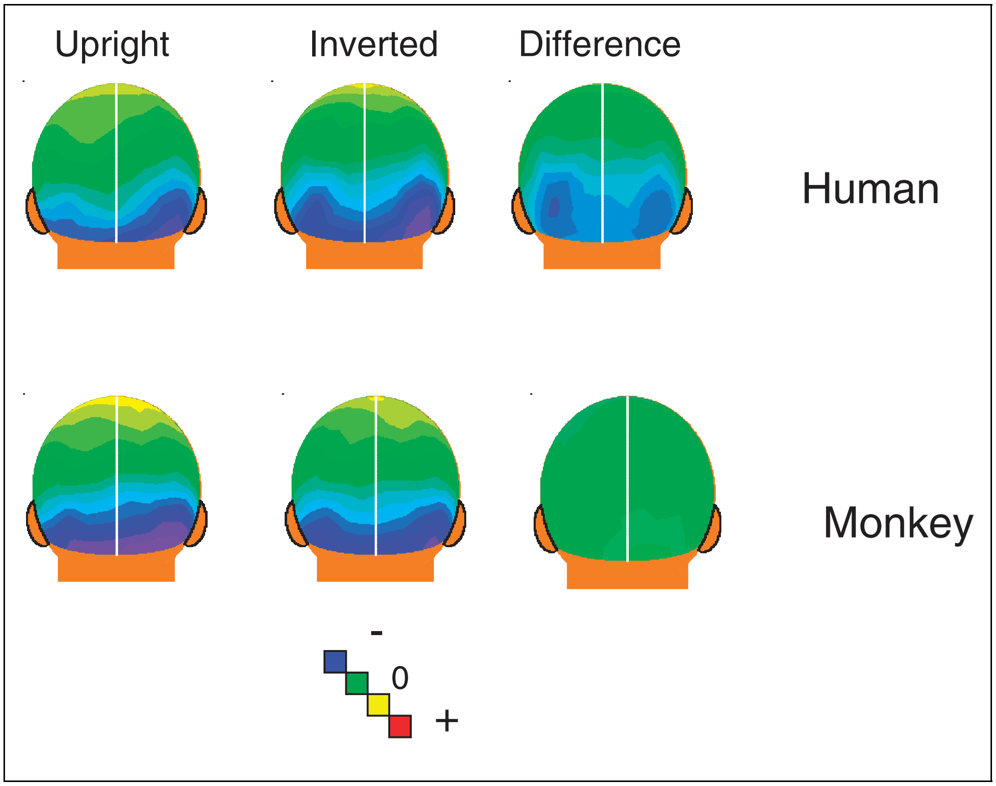
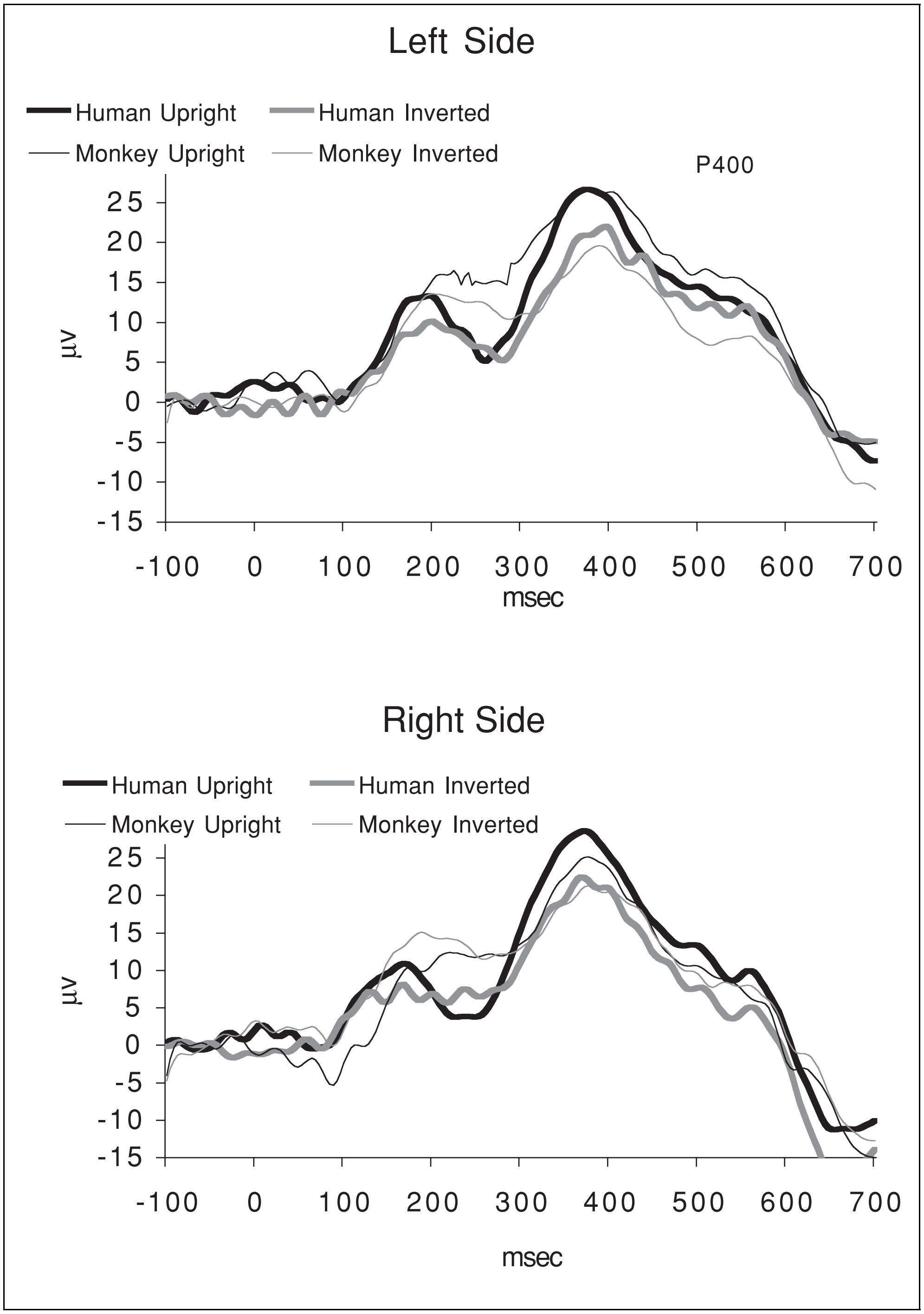


Figure 2. Spline maps of adults' grand average ERPs showing the voltage distribution at the peak of the N170 for upright and inverted human faces and the difference between the two, and for upright and inverted monkey faces and the difference between the two. Scale is from −8.5 to +8.5 μV.

Figure 3. Grand average of infants' ERPs to upright human faces, inverted human faces, upright monkey faces, and inverted monkey faces at the right posterior temporal (T6) and left posterior temporal (T5) electrodes.



interaction, $F(2,64) = 5.56$, $p < .05$]. Unlike the adult N170, there were no effects of Orientation on the amplitude of this component and no effects of Orientation or Species on the latency of this component.

The distribution of the candidate "infant N170" is shown in the spline maps of voltages in Figure 4. As can be seen by comparison with the same maps for the adult N170 shown in Figure 2 and in the waveforms illustrated in Figure 5, the infant component decreased in amplitude from medial to lateral sites more markedly than did the adult N170.

Following this negativity, the P400 component reported in previous studies of infants' ERPs to visual stimuli (e.g., de Haan & Nelson, 1999) was observed. The P400 was elicited over occipito-temporal sensors by both upright and inverted human and monkey faces and, like the other components, decreased in amplitude from medial to lateral recording sites [Main effect of

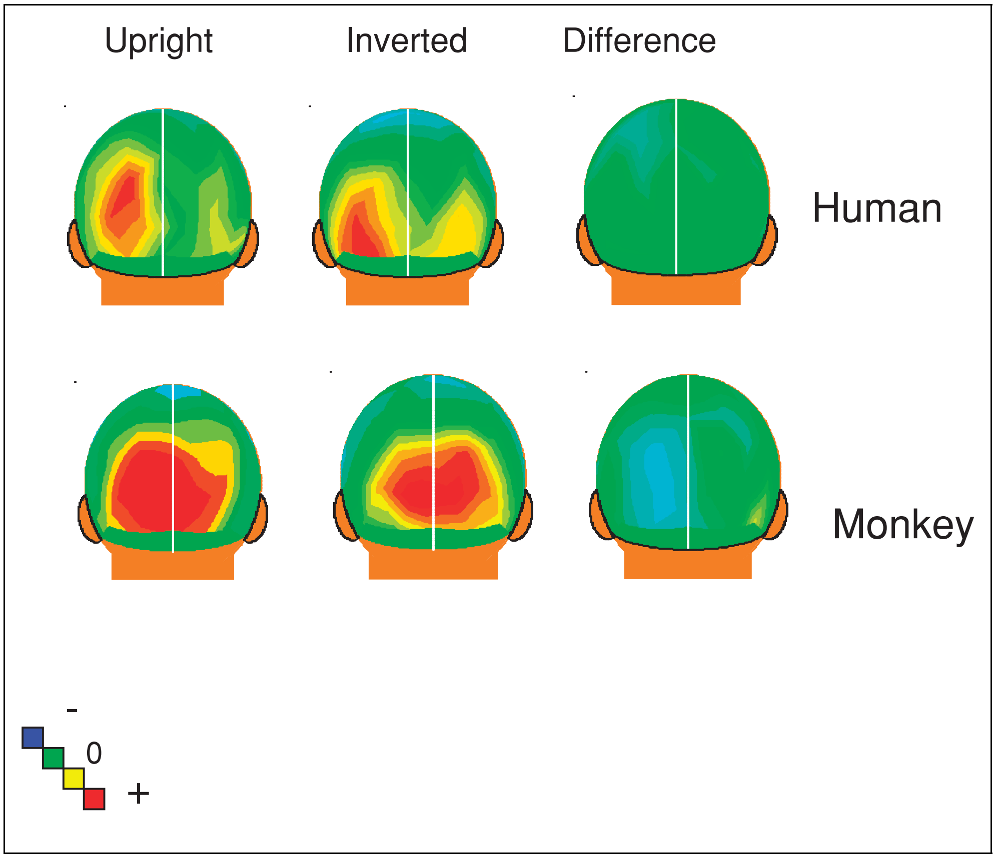


Figure 4. Spline maps of infants' grand average ERPs showing the voltage distribution at the peak of the "N170" for upright and inverted human faces and the difference between the two, and for upright and inverted monkey faces and the difference between the two. Scale is from −18 to +18 μV.

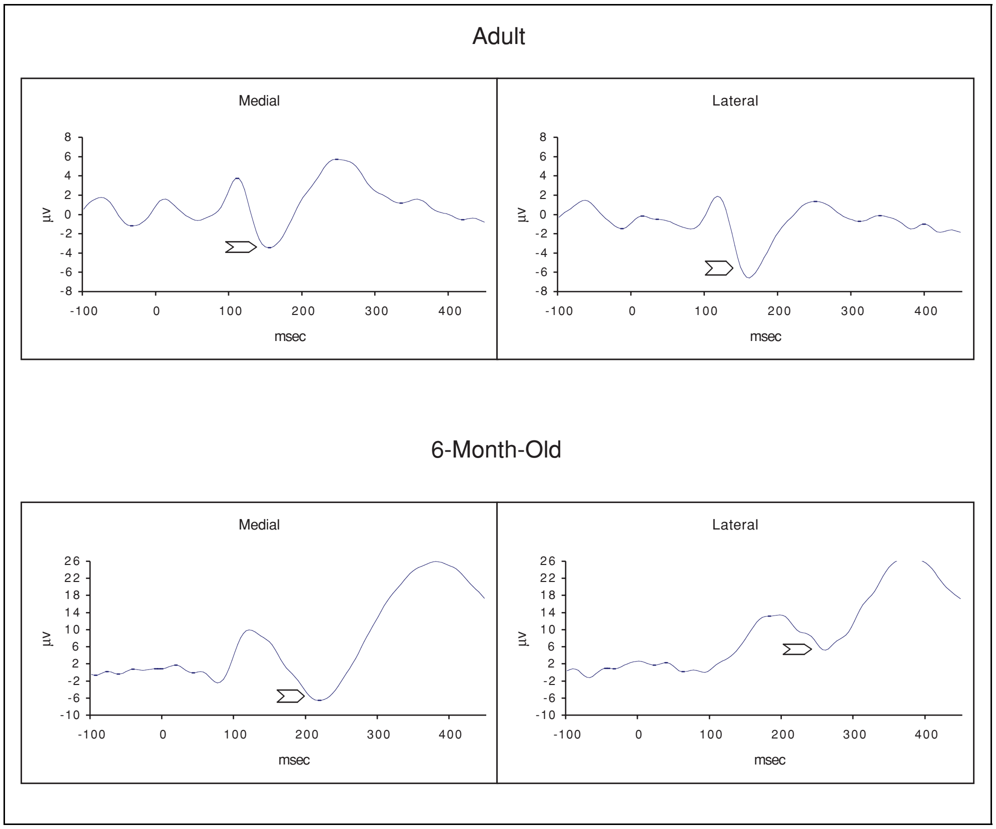


Figure 5. Grand average ERPs for infants and for adults showing amplitude and latency of the N170 component at medial and lateral electrodes.

Electrode, $F(2,64) = 7.79, p < .01$]. The P400 was largest at left, medial recording sites [Electrode × Hemisphere interaction, $F(1,32) = 5.45, p < .05$], and it peaked more quickly at medial than lateral electrodes [Main effect of Electrode, $F(2,64) = 6.57, p < .05$].

The peak amplitude of the P400 was influenced by the orientation of the face [Main effect of Orientation, $F(1,32) = 7.49$, $p = 0.01$]: Both human and monkey faces showed larger amplitudes of the P400 for upright compared to inverted faces (see Figure 3 and spline maps in Figure 4). The effect of Orientation was largest at left, medial recording sites [Orientation × Hemisphere × Electrode interaction, $F(1,32) = 8.89$, $p < .01$]. The topography of the inversion effect differed for the human and monkey faces [Species × Orientation × Hemisphere interaction, $F(1,32) = 5.12, p < .05$]. The inversion affected P400 amplitude only over the left side for monkey faces [Orientation × Hemisphere interaction, $F(1,16) = 6.68$, $p < .05$], but over both left and right sides for human faces (see Figure 3). The effect of inversion was larger at medial than lateral sensors for human faces, but was equal over the two regions for monkey faces [Species × Orientation × Electrode interaction, $F(1,32) = 5.99, p < .05$].

In summary, in 6-month-old infants, a component with similar morphology to the N170 was elicited that showed some sensitivity to the human face in that it was of larger amplitude to human than to monkey faces. However, it differed from the adult N170 in that: (a) it peaked approximately 100 msec later than the adult N170; (b) its amplitude to human faces was approximately 6 μV smaller than the adult N170; (c) it was not influenced by stimulus inversion; and (d) it showed a more marked decrease in amplitude from medial to lateral sites than the adult N170. Following this component, a P400 was elicited that was influenced by stimulus inversion: It was larger for upright than inverted faces, regardless of species. There were some differences between species in the distribution of this effect, with the difference largest over the left side for monkeys but largest bilaterally at medial sensors for human faces.

DISCUSSION

The main purpose of this study was to establish whether infants show the same degree of specificity of cortical activation during face processing as do adults. The specificity of the adult N170 recorded over occipito-temporal sensors was demonstrated by its unique response to upright human faces: It was of smaller amplitude and shorter latency than for inverted human faces or monkey faces. At no single time point in the infant ERP was there a similar sensitivity to both the species and orientation of the face. However, we observed two components in the infant ERP that were influenced by only the species or only the orientation of the face. The putative "infant N170" was identified on the basis of being a negative deflection over occipito-temporal electrodes that followed the P1 and peaked at a slightly longer latency than the adult N170. The infant N170 differs from the adult in its slower peak latency, its more medial distribution and its somewhat smaller amplitude response to human faces (8–16 μV in adults; 2–10 μV in infants following a larger amplitude P1). The infant N170 was larger for human than monkey faces. Following the infant N170, we observed the P400, a component that a prior study reported to be of shorter latency for faces than for objects (de Haan & Nelson, 1999). In the present study, the P400 was larger for upright than inverted faces.

For adults, while an N170 was elicited by all stimuli, contrast analyses and comparison of the spline maps show that the response to upright human faces was unique and that the response to monkey faces more closely resembled that to the inverted human face (see Figure 2). fMRI studies with adults indicate that face-sensitive regions of the cortex, such as the so-called fusiform face area, are activated not only by upright human faces but also by inverted faces as long as the stimuli are recognizable as faces (Kanwisher et al., 1998). However, the response to inverted faces differs from that to upright faces in that the former appear to activate additional areas of the cortex involved in object recognition, which often lie adjacent to face areas (Haxby et al., 1999). Thus, in adults, stimuli that are recognizable as faces, but are not upright human faces (i.e., monkey faces, inverted human faces), may engage both face-sensitive regions and additional object processing regions. This may be why they elicit a larger amplitude N170 than the upright human face, since at least two adjacent sources are contributing to the component.

At no point in time did the infant ERP show the same degree of specificity to upright human faces as the adult N170. This was not because infants were unable to process the species or orientation of the faces. Infants showed sensitivity to both of these factors, but, unlike adults, their processing of these factors was separated in time. The infant N170 was affected only by the species of the faces and was larger for human than for monkey faces. This suggests that the generators underlying the putative infant N170 are activated more by human than nonhuman faces. In adults, the N170 is larger for faces than for objects (Bentin et al., 1996). The larger infant N170 for human than monkey faces might occur because infants process the monkey faces more like objects than like faces.

There was no influence of inversion on the infant N170. In adults, the N170 is considered to reflect aspects of structural encoding of faces, or identifying a stimulus as belonging to the category of "face" (Bentin et al., 1996). For adults, the orientation of the face appears to play a role in this early phase of processing (Eimer, 2000), but for 6-month-old infants, the influence of orientation appears only at a later phase of processing. The absence of an influence of inversion on the infant N170 is consistent with the hypothesis that the generator(s) develop the adult pattern of specialization for face processing (including both species and orientation) through experience. Part of the mechanisms of specialization may involve an increasingly detailed specification of an early category-detection phase of processing to allow only particular inputs (face, letters, etc.) to be guided into the most efficient route for recognition of individual identity. Arguably, at 6 months, infants have been exposed to many upright human faces but not to a sufficient extent, or to a sufficient range of faces, to elicit an ''inversion effect.'' A recent study with adults showed that intensive perceptual training in recognition of 3-D forms (greebles) results in the emergence of an inversion effect on the N170 elicited by these forms (Rossion et al., 2000a). Preliminary evidence from our laboratory suggests that, by 12 months of age, the infant N170 is larger for inverted than upright human faces (Halit, de Haan, & Johnson, unpublished data). Together, these results support the view that experience drives the specialization of the N170. Whether this experience is necessary during certain stages of development or can occur at any point in the lifetime is uncertain. However, the results of a recent behavioral study of face recognition in children and adults who had previously undergone surgery to remove bilateral cataracts suggests that visual experience in the first half year of postnatal life is essential for normal development of face recognition (Le Grand, Mondloch, Maurer & Brent, 2001). Further research comparing the acquisition of specialization for face processing during development with the acquisition of expertise in adulthood is needed to determine whether the mechanisms underlying specialization resulting from experience are the same for the developing and mature system.

Is the component that we identified in infants really comparable to the adult N170? The similarities between the two include their sensitivity to face species, their occurrence following the P1, and their posterior distribution. However, they differ in that the candidate infant N170 is of longer latency, more medial scalp distribution, and is unaffected by face inversion. The longer latency and smaller amplitude of the infant N170 compared to the adult N170 was expected given that the N170 is known to decrease in latency and increase in amplitude between 4 and 14 years of age (Taylor et al., 1999; Taylor, Edmonds, McCarty, & Allison, 2001). The difference in scalp distribution is perhaps also not surprising. The infant's skull is thinner, and at 6 months, the fontanelle is not yet fully closed, both factors that can affect the distribution of scalp-recorded activity (e.g., less impedance due to the fontanelle might cause the more medial distribution). Another possibility is that there are developmental differences in the generator(s) underlying the N170. For example, it has been proposed that ventral/medial occipito-temporal areas respond more to whole faces than face parts and may be more involved in processing information about facial identity, while lateral temporal areas respond more to some face parts (e.g., eyes) than whole faces and may be more involved in processing information about facial gesture and other communicative information (e.g., emotion, eye gaze; Puce, Allison, Bentin, Gore, & McCarthy, 1998). If both areas normally contribute to the adult N170, the difference in topography of the infant N170 may reflect differential maturation of these different functional cortical areas. This could be tested in future studies comparing stimuli that in adults appear to differentially activate these regions (e.g., whole face vs. parts). In addition, further developmental studies with older infants can establish whether the component that we have tentatively identified as the infant N170 is, in fact, the developmental precursor of the adult N170. If future evidence supports this view, the infant N170 could prove a valuable tool for investigating the infant precursors of developmental disorders involving atypicalities in social information processing.

While the infant N170 was not influenced by the orientation of the face, infants did process this information: The P400 following the N170 was larger for upright than inverted faces. Thus, the influence of orientation was similar for infants and adults in that there was a greater relative negativity for inverted compared to upright faces, but this effect occurred approximately 220 msec earlier for adults than for infants and was specific to human faces for adults but not for infants. A prior study also found that the infant P400 displays some functional characteristics of the adult N170: In 6-month-olds, the P400, but not earlier components, was of shorter latency for faces than for objects (de Haan & Nelson, 1999). Thus, in 6-month-olds, the P400 may in part reflect processes that at a later age are integrated into the N170. Part of the process of developmental specialization for face processing may be a more rapid and integrated processing of information relevant to category detection. If this is true, then at the age when the inversion effect emerges in the N170, it should disappear in the P400. This prediction is currently under investigation.

The differences between infants and adults in the electrophysiological correlates of face processing suggest that there may be differences in their behavioral responses to faces as well. Numerous studies have reported that inversion causes an increase in errors and/or reaction time in adults' processing of faces (Valentine, 1988). Early studies indicated that, unlike adults, children younger than 10 are as quick and accurate in recognizing inverted as upright faces (Carey & Diamond, 1977; Diamond & Carey, 1977). However, several methodological shortcomings of this work were noted, and more recent studies designed to overcome these limitations demonstrate that an inversion effect can be demonstrated even in children as young as 5 years (e.g., Pascalis, Demont, de Haan, & Campbell, 2001; Flin, 1985). These results are compatible with the small number of studies available showing that 6- to 7-month-old infants fail to show normal recognition of facial identity (Fagan, 1972) or expression (de Haan & Nelson, 1998; Kestenbuam & Nelson, 1990) when faces are inverted. Our ERP results suggest that, while inversion disrupts the behavioral recognition of faces by both infants and adults: (a) the point in processing where inversion exerts its effects may be different (later) in infants; and (b) the effect of inversion may be less specific to faces in infants than adults. However, as there are no behavioral studies that have tested infants' and adults' response to inversion of faces and other categories under the same conditions, this remains a speculation.

A central debate in the study of face processing is whether there is an innate neural mechanism specialized and devoted uniquely to human faces or whether such neural specialization is a result of acquired visual expertise. Our results are consistent with the hypothesis that, while specific areas and pathways are engaged by faces from the first months of life, their response properties change during postnatal development. Regardless of whether the component we identified as the infant N170 is, in fact, the precursor to the adult N170, the main finding remains that at no point in the infant ERP did we see the pattern of component response observed in the adult N170. Rather, the functional specificity of the adult N170 is "smeared" across two different components in the infant. Current findings suggest the intriguing possibility that some aspects of the development of specialization of face processing may resemble the consequences of intensive training in adult perceptual learning experiments. Further research is required concerning the spatial and temporal characteristics of cortical activation patterns during postnatal development in order to determine the similarities and differences in the effects of visual experience on the developing and mature system. Our results demonstrate that for the developing system, 6 months of visual experience with faces is not sufficient for the adult patterns of specialization for face processing to emerge.

METHODS

Participants

Adults

The final sample consisted of 11 right-handed neurologically normal adults (five males) with an average age of 27 years (range 19–42). An additional six adults were tested but were excluded because of excessive eye blinking during recording ($n = 4$) or technical problems ($n = 2$).

Infants

The final sample consisted of 34 six-month-old infants (18 males) with an average age of 187 ± 3 days. All were born full term and were of normal birthweights. An additional 141 infants were tested but were excluded due to excessive eye and/or body movements that resulted in recording artifacts ($n = 101$), inattentiveness/falling asleep ($n = 19$), or technical problems ($n = 21$). This relatively high attrition rate was due to our strict standard for obtaining sufficient trials to include in ERP averages.

Stimuli

The stimuli were 20 images each of human faces (supplied by D. Maurer and S. Geldart, McMaster University) and monkey faces shown against a grey background.

Procedure

Participants passively viewed the faces while seated in an accoustically and electrically shielded sound booth. All adults viewed both species of face in both orientations. Each of the 40 unique images was shown four times in the upright orientation and four times in the inverted orientation. Adults also saw 20 unique images of sheep faces shown four times in each orientation, but because infants were not tested with these stimuli, these data are not presented. The order of presentation was random with the constraints that each unique image in the set appear once before any was repeated and that the same orientation was not repeated more than three times in succession. For infants, half ($n = 17$) viewed human faces in both orientations, and the other half viewed monkey faces in both orientations. The two orientations were shown with equal probability, and the order was randomized with the same constraints as for adults. If needed, the experimenter activated a noise between stimulus presentations via a loud speaker located out of site beneath the presentation monitor to reorient the infant's attention. Infants continued viewing the stimuli until they became too fussy or bored to attend. The average number of trials viewed for human faces was 138 trials (range 97–180), and for monkey faces, it was 103 (range 85–160).

EEG was recorded using a Geodesic Sensor Net (Tucker, 1993) consisting of 63 (for infants) or 129 (for adults) silver–silver chloride electrodes evenly distributed across the scalp. A ground electrode was positioned posteriorly above the neck for infants and on the forehead for adults. The electrooculogram was recorded from electrodes positioned above both eyes and on the outer canthi for infants and from electrodes positioned above and below both eyes and on the outer canthi for adults. All bioelectrical signals were recorded using EGI Net Amps (Eugene, OR). The signals were recorded referenced to the vertex, with a bandpass of 0.1–45 Hz and with gains set to 25,000 times. Each trial consisted of a 336-msec baseline followed by a 500-msec stimulus presentation, followed by 1164 msec during which the screen was grey. EEG was sampled every 4 msec (250 Hz) through the trial (i.e., 336 msec preevent to 1664 msec postevent).

Data Analysis

Data for each trial were truncated to create a chunk from 136 msec before stimulus onset to 700 msec after stimulus onset. Data were then digitally filtered with a 30-Hz low-pass elliptical filter and edited for artifacts. Data were excluded if they went off-scale, if the sensor was not making good contact, or if there were non-biological signals visible. The entire trial was excluded if data from more than 12 sensors had to be deleted or if there was on eye blink during any point in the trial. Eye blinks and eye movements were identified from the electrooculogram recordings and from coding of videotapes of babies during the test session.

Data were baseline corrected (i.e., the average voltage during the 100-msec preevent period was subtracted from the postevent data points), and for each participant, a separate average was computed across the trials within each condition (four for adults, two for infants). If the individual's average had less than 15 (for infants) or less than 30 (for adults) for more than four sensors, then the data were excluded from further analysis. For the remaining individuals, any missing data were interpolated using spherical spline interpolation. The average number of trials were: for infants, 26 for upright faces and 25 for inverted faces; and for adults, 68 for upright faces and 71 for inverted faces. Note that the difference in signal-to-noise due to lower numbers of trials in infants' averages is balanced by the fact that infants' visual ERPs are of much larger amplitudes (i.e., bigger signal) than adults'.

For the adult N170 (144–200 msec) and the infant "N170" (260–336) and P400 (296–460 msec), two measures were obtained: (1) peak amplitude (μV), by identifying the most negative (N170) or most positive (P400) voltage in the time window; and (2) peak latency (msec), by identifying the time point at which the peak amplitude occurred. Measures from different sensors were averaged to create four spatial groupings: right medial, left medial, right lateral, and left lateral. The sensors that contributed to these groups were (see Tucker, 1993): right medial—adults (77, 78, 79, 84, 85, 86), infants (39, 40, 41); left medial—adults (60, 61, 66, 67, 71, 72), infants (29, 36, 37); right lateral—adults (90, 91, 92, 95, 96, 97), infants (43, 44, 45); and left lateral—adults (58, 59, 64, 65, 69, 70), infants (28, 32, 35). For adults, these measures were analyzed in a 2 × 2 × 2 × 2 repeated-measures ANOVA with Species (human, monkey), Orientation (upright, inverted), Hemisphere (left, right), and Sensor Group (medial, lateral) as within-subjects factors. For infants, these measures were analyzed in the same way except that the Species factor was a between-subjects factor.

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