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Children's neural response to contrast-negated faces is species-specific

Benjamin Balas¹ and Kate Stevenson²

¹Department of Psychology, North Dakota State University, Fargo, ND

²Department of Psychology, Concordia College, Moorhead, MN

Abstract

Face recognition abilities develop dramatically during the first year of life, but comparatively little is known about the nature of face-specific perceptual development in early childhood. Face-specific effects of image appearance on recognition, including face inversion and contrast negation, are a useful means of understanding the functional properties of face perception developmentally. Here, we examined the generality of the impact of contrast-negation on face perception in early childhood using event-related potentials (ERPs). Specifically, we recorded continuous EEG while adult participants and children between the ages of 4–6 years old viewed human and non-human primate faces presented either in positive or negative contrast. We examined both the P100 and N170 components to determine whether or not sensitivity to contrast polarity was evident in face-sensitive components in early childhood, and also whether or not that sensitivity was specific to species category. We find evidence of a species-specific effect of contrast negation at the N170, suggesting that by early childhood some aspects of face-specific processing have been restricted to a relatively narrow class of face stimuli. However, this effect is of opposite sign relative to adults, suggesting that there is continued maturation of face-specific processing during childhood.

Keywords

Face Perception; Contrast Negation; Event-Related Potentials; Visual Expertise

Introduction

Face processing, besides being functionally distinct from object processing, is also affected by the category membership of face stimuli. The most well-known examples of how face recognition and face discrimination differ as a function of experience-defined categories are the effects of race (Meissner & Brigham, 2001) and species (Dufour et al., 2004) on performance. Briefly, faces belonging to groups that observers have infrequent contact with tend to be remembered poorly, to be difficult to distinguish, and to look more homogeneous than faces that resemble those observers have more frequent contact with. A lack of experience with a particular category of faces not only compromises raw recognition and

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Corresponding Author: Benjamin Balas, Department of Psychology, North Dakota State University, Fargo, ND 58102, Phone: 701-499-5276, Fax: 701-231-8426.

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discrimination performance, but also appears to compromise the extent to which face-specific mechanisms are applied. There are, for example, several behavioral indices of expert-level face processing that distinguish face processing from object processing: The well-known inversion effect (Yin, 1969) obtains more robustly for faces than other objects, and is also less evident for faces belonging to other-race categories (Balas & Nelson, 2010). Holistic processing of faces, as revealed by the “composite face effect” (Young, Hellawell, & Hay, 1987), also does not obtain as robustly for other-race faces as for own-race faces (Michel et al., 2006). The “part-whole effect,” another index of holistic processing that does not obtain robustly for non-face objects (Tanaka & Farah, 1993), also exhibits selectivity for experience-defined face categories (Tanaka, Kiefer, & Bukach, 2004). These behavioral results suggest that the underlying mechanisms that drive face-specific processing may not be applied as readily to faces belonging to “other” categories.

The emergence of experience-dependent face processing takes place during the first year of life. Specifically, infants follow a developmental trajectory that has been termed “perceptual narrowing” to reflect the fact that young infants are better able to discriminate between exemplars of multiple face categories than older infants (Nelson, 2001). This is evident for categories defined by race (Kelly et al., 2007) and species (Pascalis et al., 2005) and is taken to imply that the representation of face appearance has “narrowed” or converged to a state that is optimal for the subset of faces that infants see most frequently, but potentially sub-optimal for other types of faces. The effects of perceptual narrowing are evident both behaviorally and in electrophysiological data – ERP components including the N290 and the P400 are sensitive to face category membership in a manner that is broadly consistent with perceptual narrowing (de Haan, Pascalis & Johnson, 2002; Balas et al., 2011), which suggests that neural representations of face appearance are being substantially modulated by experience during the first year of life.

While the emergence of category effects on face recognition begins in infancy, many of the behavioral effects described above that distinguish face processing from object processing are evident in early childhood. The inversion effect, for example, is evident in children at 3 and 4 years of age (Sangrigoli & de Schonen, 2004), as is the part-whole effect (Pellicano & Rhodes, 2003). Holistic processing as indexed by the composite face effect is adult-like by 6 years of age (Mondloch et al., 2007) and has been observed in children as young as 4 years old (de Heering et al., 2007). Many so-called qualitative markers of expert face processing thus appear to be mature in early childhood, and may even be mature in infancy (McKone, Crookes, & Kanwisher, 2009). Selectivity within the category of faces also appears to begin developing relatively early in childhood as well and influences the impact of stimulus manipulations that selectively disrupt face recognition. For example, by three years of age children not only show better processing of own-race faces compared to other-race faces, but they also show a larger inversion effect (Sangrigoli & de Schonen, 2004). This suggests that by early childhood, at least some of the mechanisms underlying the differential processing of faces and objects may be mature, and that some categories of faces may also be processed by different mechanisms than the faces children are developing expertise for.

Our goal in the current study was to examine whether or not stimulus manipulations that affect face recognition performance manifest in early childhood in a category-dependent way. Does greater experience with one category of faces vs. another affect the extent to which neural responses to those faces are modulated by appearance manipulations that are known to affect faces more than objects? We chose to compare the impact of contrast negation on the neural response to human and monkey faces by measuring children’s ERP responses to positive and negative faces of both species. The distinction between human and monkey faces is particularly useful to consider for several reasons. Most observers have little to no experience individuating monkeys from one another, which obviates concerns

about residual experience with the out-group adding unwanted variability to the data. However, even though most observers lack experience with these stimuli and monkey faces differ substantially from human faces, there is evidence that some aspects of face-specific processing (e.g. the inversion effect) apply to some non-human primate faces nonetheless (Taubert, 2009). Compared to more phylogenetically distant face categories (like dogs or cats), non-human primate faces appear to share some qualities with human faces in terms of perceptual processing.

Contrast negation and its effects on face recognition are a particularly useful way to examine the specificity of face processing. Contrast negation typically involves the reversal of intensity values in a parent image, yielding an image where dark pixels become light, and vice versa. This transformation is known to substantially disrupt face recognition (Galper, 1970), but not the recognition of other objects (Vuong et al., 2005). Besides disrupting basic categorization and identification tasks, contrast negation also impairs a number of specific perceptual features in face images that include inter-feature distances (Kemp, McManus & Pigott, 1990), surface pigmentation (Russell et al., 2006), and 3D shape (Kemp et al., 1996). Compared to other transformations of face appearance that are commonly used in the face recognition, like face inversion or face scrambling, negation is unique in several regards: Contrast negation preserves the “first-order” configuration of the face (Maurer, Le Grand, & Mondloch, 2002), which refers to the canonical arrangement of face features within a face. Contrast negation (like face inversion) also preserves the “second-order” configuration of the face, which refers to the distances between discrete facial features. Though the *perceived* distance between these features can be substantially disrupted after negation (Kemp, McManus, & Pigott, 1990), the real physical distances are unchanged. Contrast negation also preserves the orientation energy in the original image, such that the distribution of edges across spatial scales and orientations is unchanged. The spatial layout of those edges is also preserved, which is not true for inverted face images. In sum, contrast negation is an important means of preserving a number of perceptually relevant physical features within a face image while also substantially disrupting a number of higher-order features, leading to impaired recognition. Behaviorally, there have been relatively few studies of how contrast negation affects children’s recognition of faces, the issue of category-selectivity notwithstanding. Contrast polarity affects infants’ preferential tracking of face patterns (Farroni et al., 2005) such that negated schematic stimuli do not elicit robust preferences to the same extent that positive contrast stimuli do. Adults exhibit the same behavioral profile in a continuous flash suppression paradigm (Stein, Peleen, & Sterzer, 2011), which suggests that visual awareness in adults is modulated by similar visual properties as visual preference in infancy. Older infants (7–8 months of age) exhibit effects of contrast negation on face discrimination (Otsuka et al., 2013) – discrimination between individual faces is disrupted by contrast negation, but this appears to be critically dependent on the contrast polarity of the eye region. This result is also consistent with behavioral results obtained from adult observers (Gilad, Meng, & Sinha, 2009), again suggesting that some aspects of adults’ sensitivity to contrast polarity in face images are evident in the first year of life. We have therefore opted to use contrast negation in this study as a means of characterizing the species-specific processing of face images because of its unique effects on the physical and perceptual contents of face images and the relative paucity of data concerning how children’s face recognition is impacted by this powerful stimulus transformation.

We examined children’s and adult’s ERP responses to human and monkey faces presented in positive and negative contrast, with particular attention to the P100 and N170 components. These components are reliably elicited by face images in children (Kuefner et al., 2010) and adults (Bentin, 1996) and appear to reflect distinct stages of face processing. The P100, though often described vis-à-vis low-level processing of image luminance and contrast (Nakashima et al., 2008) also exhibits some sensitivity to face appearance (Dering,

Martin, & Thierry., 2009). Convergent evidence from MEG studies of the M100 (Liu, Harris & Kanwisher) and TMS studies targeting early face processing (Pitcher et al., 2007) suggest that the P100 may reflect the initial encoding of face parts and only a coarse representation of global structure. By comparison, the N170, which has been frequently described as a sort of face detector that reflects the initial structural encoding of a face pattern (Eimer, 2000), also exhibits some sensitivity to face categories. For example, the adult N170 exhibits sensitivity to the age (Melinder et al., 2010; Wiese, 2012), race (Balas & Nelson, 2010; Wiese, 2012), and species (Itier, Van Roon & Alain, 2011; Balas & Stevenson, 2013) of visually-presented faces. Critically for our purposes, the adult N170 also responds differentially to faces presented upside-down (Rossion et al., 2000) or in negative contrast (Itier & Taylor, 2002, 2004; Itier et al., 2006,; Itier et al., 2007). The sensitivity to face categories interacts with the effects of these various transformations of the face in adult observers, as evidenced by a number of studies (Rousselet et al., 2004; Balas & Nelson, 2010). Briefly, robust effects of inversion, etc. tend to be most evident for faces that observers have the most experience with. This broad result is typically taken as evidence to support the hypothesis that the face-specific neural mechanisms that ostensibly underlie the effects of contrast negation and inversion are only applied robustly to the faces observers have accumulated the most experience with. Faces that do not belong to the experience-defined in-group are thus not subject to face-specific processing to the same degree.

In the current study, we have opted to study adults and children between 4–6 years of age, which may seem at odds with the aforementioned results suggesting that perceptual narrowing (and consequent category-dependent processing) takes place during the first year of life. If 9–12 month old infants already have a “narrow” representation of face appearance sufficient to yield other-race and other-species effects on face discrimination, why are 4–6 year old children interesting to study in this context? We argue that there are several reasons why children in this age range are of particular interest. First, while it is true that infants exhibit the first behavioral and neural signatures of experience-dependent face processing in the first year of life, that by no means implies that perceptual narrowing (or any other developmental process relevant to face recognition) is complete. For example, the fusiform face area appears to grow larger during middle childhood (Golarai et al., 2007), but the measurement of FFA volume in children is complicated by several methodological factors that may make comparison to adults challenging (McKone et al., 2012). The selectivity of the N170 component across development is relatively stable however, (Kuefner et al., 2010) supporting the possibility that a great deal of selectivity for faces relative to other objects has been established by at least early childhood. Second, in terms of differential processing of faces belonging to distinct categories, there are several behavioral results that demonstrate ongoing changes in the generality of various face-specific effects during childhood. The other-race effect remains plastic in early childhood, for example, (Sangrigoli et al., 2004), which indicates that continued adaptation to the statistics of visual experience can still impact perceptual fluency at later stages of development. The well-known left-side bias for face recognition (Burt & Perrett, 1997) also exhibits a developmental trajectory that extends into middle childhood – children do not reliably show a species-specific left-side bias favoring human faces until they are 8–9 years of age (Balas & Moulson, 2011).

The nature and scope of face processing as determined by behavioral and neural indices is thus a largely open question. Indeed, recent results have led to an ongoing debate about the nature of *any* face-specific development in childhood (Crookes & McKone, 2009). While a substantial body of prior work suggests that children undergo developmental shifts in their ability to use holistic representations of faces (Carey & Diamond, 1977; Carey, Diamond & Woods, 1980) and other face-specific mechanisms, it has been recently suggested that a number of these results are artifacts of floor effects and other methodological issues (McKone, Crookes, & Kanwisher, 2010) and that any development of face recognition in

childhood likely reflects more global cognitive development instead. While recent studies that have controlled for these methodological issues have yielded evidence for at least some limited face-specific development in childhood (Weigelt et al., 2013), there remain many unanswered questions regarding how face recognition changes during early childhood. We suggest that comparisons between faces of different categories is a particularly useful means of examining this issue, since comparisons between faces remove many of the intrinsic difficulties of selecting a comparison class of objects to compare to faces for the purposes of identifying face-specific processes. Finally, in comparing children to adults using electrophysiological methods, 4–6 year old children are a particularly useful population. Unlike infants, whose face-sensitive ERP components differ substantially from adults (de Haan, Johnson, & Halit, 2003) children in this age range produce visual ERPs in response to faces that are more similar to adults in terms of overall morphology. This is critically important, since it is otherwise difficult to know exactly how to compare the effects observed at different components. Moreover, children in this age range can be asked to perform simple behavioral tasks during EEG acquisition, leading to groups that are more clearly matched for attentional demands, etc. Finally, previous results (Itier & Taylor, 2004a; 2004b) demonstrate that older children (8–16 years old) exhibit significant effects of contrast negation on the N170 latency, but not the amplitude. This result demonstrates that there is some ongoing development in middle childhood related to the neural processing of positive vs. negative faces, and also suggests that examining younger children's responses to positive and negative faces may offer important insights into the nature of this developmental trajectory. To our knowledge, the effects of contrast-negation on the ERP responses of children younger than 8 years old have not previously been reported in the literature.

We used a simple oddball paradigm to record ERPs from adults and children in the target age range while they viewed images of humans and monkeys presented in positive and negative contrast. We wished to determine how early markers of face processing, the P100 and the N170, were modulated by contrast polarity as a function of age and face categories. We hypothesized that the effect of contrast negation in adults should be species-specific, but that children either may not have any measurable effects of negation at these components, or that the effect of negation might be the same for human faces and monkey faces. We found instead that children do indeed exhibit a species-specific effect of negation, but that the nature of this effect differs from the analogous effect observed in adults. We discuss this result in the context of related developmental ERP studies of face perception, and suggest important avenues for further research.

Methods

Subjects

We recruited 16 children (9 female) between the ages of 4;6-6;2 ($M=5;1$) to participate in this study. The caregivers of all participants indicated that each child's vision was normal or corrected-to-normal, and all participants were right-handed, as determined via the Edinburgh Handedness Inventory. Informed consent was obtained from the legal guardian(s) of each child, and each child also gave verbal assent to take part in the study.

To compare the response of children in the target age range to adults, we also recruited 14 adults (6 female) between the ages of 19 and 32 to take part in the same task. All adult participants reported normal or corrected-to-normal vision and were right-handed.

Stimuli

Our stimulus set was comprised of 6 full-color photographs of adult men and 6 photographs of macaque monkeys (Figure 1). The dimensions of the human faces were 256×256 pixels, and the macaque faces were 300×256 pixels. The difference in size is due to the monkey faces being slightly longer than the human faces. Additionally, the gaze direction of the monkey faces was more variable than that of the human faces – human faces tended to be looking straight ahead, while some monkey faces depicted gaze that was somewhat averted. Each face was cropped with a circular or oval window to exclude the jawline of faces belonging to both species and the hair of human faces. We manipulated the contrast polarity of each image using the GIMP image editing application. Specifically, we inverted the pixel values of each face such that both luminance and hue were negated. Finally, a set of 4 cartoon images depicting colorful mushrooms were selected as target stimuli for the go/no-go task we asked participants to carry out during EEG recording. These images were 256×256 pixels in size.

Procedure

Following application of the sensor net, participants sat in a sound-isolated, darkened room approximately 50cm away from the display. At this viewing distance, each image subtended approximately 3 degrees of visual angle. Children were either seated on their guardian's lap, or sat by themselves in an adjustable chair which was raised or lowered so that stimuli were presented at approximately eye level. We presented our images to participants using custom routines written in EPrime v2.0. On an individual trial, a single image was presented on a medium-gray background for 500ms. Participants were asked to press a large plastic button if the image was a picture of a cartoon mushroom, and to refrain from pressing the button in all other instances. The incidence of these target images was fully randomized. During EEG recording, an experimenter sat in the testing room and ensured that stimuli were only presented when the participant was looking at the screen. Obviously this was less necessary for adult participants, but we followed the same procedure in both cases. For children, this procedure led to a highly variable ISI between stimuli, since some children took breaks during recording or were briefly distracted between trials. The minimum ISI between image presentations was 1200ms, but in some instances was several seconds long.

We presented participants with 48 images per condition (8 repetitions of 6 unique faces per species) yielding a total of 192 images of human and monkey faces rendered in positive and negative contrast. Participants also viewed 32 instances of the target images for a grand total of 224 trials. Image order was fully randomized and participants completed the experimental session in a single block of trials.

ERP recording and analysis

We recorded event-related potentials (ERPs) with a 64-channel Hydrocel Geodesic Sensor Net v2.0, (Electrical Geodesics Inc., Eugene, OR). We recorded EEG continuously, referenced to a single vertex electrode (Cz). We amplified the raw signal with an EGI NetAmps 200 amplifier using a band-pass filter of 0.1–100 Hz and a sampling rate of 250 Hz. Before each session, we measured impedances online to establish stable impedances below a threshold of 100kΩ.

After the conclusion of the experimental session, we used NetStation v4.3.1 (Eugene, OR) to process the continuous EEG data from each participant. We filtered the raw data with a 30-Hz lowpass filter and subsequently segmented individual trials at stimulus onset to include a 100ms pre-stimulus baseline period as well as a 900ms post-onset period, yielding segments that were 1000ms long for each trial. We applied baseline-correction to these segments by calculating the average voltage measured during the pre-stimulus period for each trial and

subtracting this value from the entire waveform. We manually marked individual channels and/or entire trials that contained obvious ocular artifacts, including blinks and saccades, and also rejected trials based on the observation of drift, excessive high-frequency noise, or a high proportion of rejected sensors (<7 channels out of 64). Next, we replaced the data from rejected sensors using spherical spline interpolation. Finally, we averaged segments within each experimental condition and re-referenced the data from each subject to an average reference. We retained data from all participants who yielded at least 30 trials per condition after post-processing (average trials per condition across these participants was ~40), and rejected the data from 3 children whose data did not meet this criteria. We also rejected the data from one adult participant who did not comply with task instructions. Thus, our analysis was carried out with 13 participants in each age group.

Results

We defined sensors of interest and component-specific time windows to analyze these two components based on visual analysis of the grand average ERPs obtained by combining the data across participants and all experimental conditions. We chose 6 occipito-temporal channels (3 per hemisphere, constrained for symmetry across the midline) as the sensors of interest for these two components, the location of which are largely consistent with previous reports (Itier & Taylor, 2004a; 2004b). While we were able to use the same sensor groups to analyze the data collected from children and adults, the differing morphology of the ERP waveform across age groups necessitated the selection of time windows that were specific to each age group. To analyze the data from our child participants, we defined a time window of 120 ms – 180 ms for analysis of the P100 and a time window of 200 ms – 320 ms for our analysis of the N170. These time windows are somewhat later and wider than the time windows typically used for adult participants (Rossion & Jacques, 2008), but are consistent with the temporal characteristics of the P100/N170 waveform complex observed in children (Kuefner et al, 2010). For adult participants, we defined a time window of 80–120 ms for analysis of the P100 and a time window of 150–190 ms for the analysis of the N170. Within these time windows, we characterized each participants' response via the mean amplitude of the component. We did not calculate either the peak amplitude or the latency to peak of these components, since children's waveforms were typically fairly broad and peak values were likely to be highly susceptible to noise (Luck, 2005). Though such an analysis would be appropriate for the data collected from adults, we report only the data from an analysis of the mean amplitude here so that we may directly compare children and adults using the same analysis. Finally, the mean amplitudes of each component were analyzed using a 2×2×2×2 mixed-design ANOVA with face species (human or monkey), contrast polarity (positive or negative) and hemisphere (left or right) included as within-subjects factors and participant age (child or adult) as a between-subjects factor. In Figure 2, we display children's grand average ERP waveforms for each condition, presented separately from the left and right hemisphere (averaging over the individual channels in each hemisphere). In Figure 3, the same data is presented for adult participants.

P100 Mean Amplitude

We observed no main effects of species category ($F(1,12)=1.187$), contrast polarity ($F<1$) or hemisphere ($F<1$). We did observe a main effect of participant age ($F(1,24)=73.64$, $\eta^2=0.54$, $p<0.001$), driven by significantly larger amplitudes in our child participants.

We also obtained a significant interaction between species category and contrast polarity ($F(1,24)=5.09$, $\eta^2=0.175$, $p=0.034$), such that the difference between responses to human and monkey faces was significant when faces were presented in positive contrast ($M_{\text{human}}=5.43\mu\text{V}$, $M_{\text{monkey}}=6.51\mu\text{V}$), but not when these faces were presented in negative contrast ($M_{\text{human}}=5.94\mu\text{V}$, $M_{\text{monkey}}=5.59\mu\text{V}$). This was qualified however, by a three-way

interaction between species, contrast polarity, and age ($F(1,24)=5.69$, $\eta^2=0.192$, $p=0.025$). Post-hoc tests (paired-sample t-tests, two-tailed) revealed that this three-way interaction resulted from adult participants exhibiting no differences between species for either positive or negative contrast, but children exhibiting a polarity-dependent difference between human and monkey faces: Monkey faces elicited larger amplitudes than human faces when presented in positive contrast ($M_{\text{human}}=8.04\mu\text{V}$, $M_{\text{monkey}}=10.42\mu\text{V}$), but exhibited no such difference when faces were presented in negative contrast ($M_{\text{human}}=9.12\mu\text{V}$, $M_{\text{monkey}}=8.53\mu\text{V}$).

Finally, we also observed a significant interaction between contrast polarity and hemisphere ($F(1,24)=5.02$, $\eta^2=0.173$, $p=0.035$), which was driven by significant hemispheric differences for negative faces ($p<0.01$), that did not obtain for positive faces.

N170 Mean Amplitude

We observed a main effect of species category ($F(1,24)=14.39$, $\eta^2=0.375$, $p=0.001$), such that the mean amplitude of the N170 was larger (more negative) for human faces than for monkey faces ($M_{\text{human}}=-0.40\mu\text{V}$, $M_{\text{monkey}}=1.41\mu\text{V}$). We observed no main effect of contrast polarity ($F(1,12)=1.60$, $p=0.22$) and no main effect of hemisphere ($F(1,12)<1$). As in our analysis of the P100, however, we did also observe a main effect of participant age ($F(1,24)=16.36$, $\eta^2=0.40$, $p<0.001$), such that adult participants had more negative N170 amplitudes ($M=-2.20\mu\text{V}$) than children ($M=3.21\mu\text{V}$).

We also observed significant interactions between species and contrast ($F(1,24)=60.45$, $\eta^2=0.33$, $p=0.002$) and between species and age ($F(1,24)=9.85$, $\eta^2=0.29$, $p=0.004$). These interactions were both qualified by a three-way interaction between species category, contrast polarity, and age ($F(1,24)=36.9$, $\eta^2=0.61$, $p<0.001$). Post-hoc tests (paired-samples t-tests, two-tailed) revealed that this interaction resulted from age-dependent differences in the effect of contrast polarity on human faces: Adults exhibited larger (more negative) amplitudes for negated human faces ($M=-2.91\mu\text{V}$) compared to positive human faces ($M=-1.80\mu\text{V}$, $p=0.0075$), while children exhibited more positive amplitudes for negated human faces ($3.29\mu\text{V}$) compared to positive human faces ($M=-0.173$, $p<0.001$). Neither children ($p=0.22$) nor adults ($p=0.095$) exhibited significantly different responses to monkey faces as a function of contrast polarity. Contrast-polarity thus appears to more strongly affect human faces than monkey faces, but induces opposite effects on the mean amplitude of the N170 as a function of age.

Finally, we also observed a significant interaction between contrast polarity and hemisphere ($F(1,24)=18.241$, $\eta^2=0.26$, $p=0.008$) that was qualified by a three-way interaction between contrast polarity, hemisphere, and age ($F(1,24)=16.84$, $\eta^2=0.24$, $p=0.010$). Post-hoc tests (paired-sample t-tests, two-tailed) revealed that this interaction was the result of significant hemispheric differences for negated faces in children ($M_{\text{left}}=2.19\mu\text{V}$, $M_{\text{right}}=4.71\mu\text{V}$, $p<0.01$) that were not realized in any other condition.

Discussion

Our data suggests that children and adults both exhibit species-selective effects of contrast polarity on the neural response to faces. However, as our interactions between species, contrast polarity, and age reveal, children do not exhibit the same species-specific effects that adults do. To speak to the stated goal of our study, our results reveal that there is continued maturation of species-specific processing between the target age range of 4–6 years old and adulthood. Broadly speaking, our results are thus consistent with previous reports of extended plasticity of category-specific processing (Sangrigoli et al., 2005; Bar-Haim et al., 2006; Scott & Monessen, 2010) and suggest that various forms of differential

processing of faces belonging to different species (Balas & Moulson, 2011) or other categories may only reach full maturity late in childhood. We continue by discussing our electrophysiological results in the context of related studies of developmental ERPs and ERP studies conducted with adults.

At the P100, we observed that children's P100 amplitude differed as a function of species category, but only for faces presented in positive contrast. Adults exhibited no such difference. The P100 is known to be sensitive to face inversion in childhood (Taylor, Batty, & Itier, 2004), and to the extent that we anticipate other species faces to be either more difficult to process (Dering et al., 2011) or to be processed in a less configural or holistic manner, we suggest that our results are not entirely unexpected. The P100 is also known to be sensitive to a number of low-level image properties, however, and so it is difficult in the current study to tease apart the contribution of high-level and low-level image content on this effect. Perhaps most importantly, the profile of results observed at the P100 appears to be different than those observed at the N170, which suggests that we are not merely measuring the same processes across two temporal windows.

At the N170, we found that both children and adults showed an effect of contrast polarity for human faces, but not monkey faces. Critically, however, the direction of this effect was not the same: The adult N170 was of greater amplitude (more negative) for negative human faces, while the child N170 was of less amplitude (more positive) for negative human faces. As such, while it is fair to say that contrast negation is species-selective in each group, we cannot conclude that the neural responses of 4–6 year olds in this task are “mature” or “adult-like.” The results obtained with adults are in good agreement with previous reports describing the impact of contrast negation on human faces (Itier & Taylor, 2002) and also with recent data describing the impact of pigmentation negation on faces of different species (Balas & Stevenson, 2013). We note, however, that the current results, as well as the results reported in Balas & Stevenson (2013), differ from Itier et al.'s (2006) comparison of negation effects to human and ape faces. Specifically, in their work, they reported smaller N170 amplitudes for negative vs. positive ape faces, which differed from the larger N170 amplitudes observed for negated human faces. This discrepancy may be the result of task differences (an oddball task in the current study compared to an orientation judgment in Itier et al., 2006) and stimulus differences, however, suggesting that continued investigation of species-selective responses in adult ERPs is warranted. To interpret the data from children, particularly the opposite-signed effect of contrast polarity on human faces, we must consider the results of several previous developmental studies that include behavioral and ERP results. To our knowledge, there is not existing data about the impact of contrast negation on the N170 of 4–6 year old children, but by synthesizing data describing how inversion impacts the N170 as a function of age with behavioral and neural data from older children, we find that our results are consistent with prior work describing an important period of development in middle childhood that affects face processing.

First, we consider Itier & Taylor's (2004a) study of the impact of face inversion and negation on ERP responses measured in children between 8–16 years of age. Obviously this sample is older than the children we recruited, but nonetheless, their data provides an important point of reference for our work. They found that adult-like effects of inversion and negation on the N170 latency were evident at all ages, but that the N170 amplitude did not vary as a function of face type for their youngest group of participants (8–9 year olds). This suggests that between 8 years of age and adulthood, the neural sensitivity to contrast negation is still maturing. This of course does not speak to the *reversal* of the effect that we observed in our participants – why should this be the case? If we consider face inversion to be a meaningful proxy for contrast negation, there is precedent for this developmental trajectory in several related studies. Behaviorally, the effects of face inversion and contrast

negation are fairly similar when compared directly in older children (Itier & Taylor, 2004b), and in adults these two manipulations lead to similar effects on face-sensitive ERP components (Itier & Taylor, 2002). Therefore, we suggest that considering how the impact of face inversion on the N170 changes with development is a useful way to contextualize the current results. Notably, the N170 amplitude appears to exhibit the same “flipped” effect relative to adults in some cases. Melinder et al. (2011) found an opposite-sign effect of face inversion in 5-year old children at the N170, for example. Similarly, Taylor, Batty & Itier (2004) report a meta-analysis of multiple ERP studies that includes data from Taylor et al. (2001) demonstrating a smaller (more positive) N170 amplitude for inverted faces measured in 4–5 year olds. Considering the data from a wider age group, it appears that a crossover point occurs somewhere in the neighborhood of 10–11 years of age, after which the adult-like inversion effect obtains. We thus suggest that our own result is consistent with previous results from children in the target age range, and is suggestive of a general developmental trend whereby sensitivity to some transformations of facial appearance may be manifest as opposite-sign effects relative to adult responses. Moreover, the current study further suggests that this process is species-specific, and does not impact faces irrespective of category membership and experience. Why does this substantial change in the N170 amplitude occur? At present, we can only speculate and we note that Taylor et al. (2004) do not offer much discussion of this feature of their data either. A possibility they raise, however, is that the frequent “bifid” appearance of the child N170 may indicate the presence of two separate sub-components that reflect different aspects of face processing. The change in sign of the effect of inversion they observe, as well as the similar change we observe for negation, may result from changes in the relative contribution of these components between early childhood and adulthood. However, the stability in the response to upright vs. phase-scrambled faces across early and middle childhood (Kuefner et al., 2010) suggests that this is not a universal property of face-specific effects in the developing brain. We suggest that understanding the nature of these “flipped effects” is a particularly intriguing challenge for continued investigations of developmental ERPs, and would benefit substantially from concerted study.

An important feature of our stimulus set that may have contributed to the species differences we have observed (in particular the main effect of species on the N170 amplitude) is the variability of gaze direction in our monkey faces relative to the human faces we used here. Specifically, our images of human faces depicted individuals looking directly at the camera while our images of monkeys depicted more variable gaze directions. In Figure 1, for example, we can see that while both the human and monkey are looking at the camera, the monkey’s head is slightly averted. While our monkey faces did mostly depict gaze toward the camera, the position of the head and eyes did vary somewhat. Gaze direction is of course a critically important component of social vision and face-specific ERP responses to inverted and negated faces depend critically on the eye region (Itier et al., 2007). To expand upon this result briefly, the impact of face inversion and contrast negation on the adult N170 is greatly reduced when the eyes are removed from the face, suggesting that the eye region (and thus eye-selective neurons) are vital components of face-selective responses. In the context of our task, one concern is thus that the larger variability of gaze direction in monkey faces may have led to differential ERP responses simply due to the varying appearance of the eye region in one species. If we adopt Thierry et al.’s (2007a; 2007b) suggestion that perceptual variability can induce amplitude differences simply by introducing larger “jitter” in the single-trial waveforms, we might easily suspect that amplitude differences should obtain at early components as the result of perceived gaze making a large contribution to the ERP response. This account is in fact consistent with the more negative amplitudes we observed in the human face condition – greater inter-trial variability for monkey faces would in principle lead to less negative amplitudes for monkey faces. We note however, that Taylor et al. (2001) demonstrated that the amplitude of adult’s

early ERP components was not affected by the gaze direction (forward vs. left-looking) of human faces, but that closed eyes did modulate ERP amplitudes. Similarly, Ponkanen et al. (2010) found that averted gaze only affected the ERPs elicited in response to live faces and that gaze direction did not modulate the ERPs elicited by pictures of faces. Further, this basic account of how gaze variability might impact our results does not make obvious predictions about how age and stimulus contrast should interact with species category. To the best of our knowledge, there are not detailed studies examining all of these factors for us to draw strong conclusions about the present results. Finally, we are confident that the variability in our stimuli was still relatively small (no monkeys exhibited fully averted gaze), which we suggest likely reduces the potential impact of gaze variability somewhat. Nonetheless, we acknowledge that this is an important factor for us to consider when interpreting the current results and a topic that deserves more detailed investigation. A controlled set of monkey faces with gaze direction either closely matched or parametrically varied would be highly useful for examining this issue in depth.

Our use of contrast negation with human and non-human primate faces has revealed some intriguing properties of the developmental trajectory of face-sensitive ERPs. We suggest that our data also suggests another direction for continued investigation of the specificity of face processing over early childhood, particularly with regard to the impact of negation on face processing. Specifically, the N170 response to faces, both humans and non-human primates, appears to depend largely on the presence or absence of the eyes (Itier, Latinus, & Taylor, 2006; Itier, Van Roon & Alain, 2011). Indeed, the effects of negation on face recognition behaviorally (Gilad, Meng & Sinha, 2009) and electrophysiologically (Itier et al., 2007) critically depend on eye appearance. When does this sensitivity to the eyes in particular emerge? Children in our study exhibited a clear negation effect for human faces, but we cannot speak at present to the contribution of specific facial features to that overall effect. Examining how the negation effect we observed here achieves this spatial specificity is another way to consider the overall development of face-specific effects in terms of convergence onto a limited class of stimuli and stimulus features.

Conclusions

The impact of contrast negation on the N170 is evident in early childhood, though the direction of the effect differs from what is typically observed in adults. The negation effect is also species-specific, indicating that whatever differential processing leads to a face-specific effect of negation, this process is not equally applied to non-human primate faces in early childhood. These results support the early development of a relatively narrow representation of face appearance that excludes out-group faces and constrains the mechanisms that are applied to them, but also suggests that there is continued maturation of face-specific neural processing between early childhood and adulthood.

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Highlights

- We measured N170 responses to own- and other-species faces in adults and 4–6 year-old children.
- Human and monkey faces were presented in positive and negative contrast.
- The N170 was only affected by negation in human faces.
- Species-selective face processing is evident in early childhood.

Figure 1.
Examples of the stimuli used in our task. Original human and macaque faces were cropped and presented to our participants in positive and negative contrast.

Figure 2. Grand average ERP waveforms from child participants, measured at occipitotemporal sites in both the left and right hemisphere.

Figure 3. Grand average ERP waveforms from adult participants, measured at the same occipitotemporal sites in the left and right hemispheres selected for the analysis of children's ERPs.