Neuropsychologia 51 (2013) 1794–1801

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Species-specific effects of pigmentation negation on the neural response to faces

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ARTICLE INFO

Article history:
Received 27 September 2012
Received in revised form
25 April 2013
Accepted 28 May 2013
Available online 20 June 2013

Keywords:
Face perception
Contrast Negation
Event-Related Potentials
Visual Expertise

ABSTRACT

Face processing is limited in scope as a function of experience – discrimination ability and face-specific behavioral effects are reduced in out-group faces. Nonetheless, other-species faces phylogenetically close to our own may be processed by similar mechanisms as human faces. Presently, we asked whether or not the well-known effect of contrast-negation on face recognition (Galper, 1970) was exclusive to human faces or generalized to monkey faces. Negation disrupts face pigmentation substantially, allowing us to examine species-specific use of surface cues as a function of expertise. We tested adult observers behaviorally and electrophysiologically: participants completed a 4AFC discrimination task subject to manipulations of face species and independent negation of image luminance and image chroma, and the same stimuli were used to collect event-related potentials in a go/no-go task. We predicted that expertise for human faces would lead to larger deleterious effects of negation for human faces in both tasks, reflected in longer RTs for correct responses in the discrimination task and species-specific modulation of the N170 and P200 by contrast-negation. Our results however, indicate that behaviorally, luminance and chroma negation affect discrimination performance in a species-independent manner, while similar effects of contrast-negation effects are evident in each species at different components of the ERP response.

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1. Introduction

Face recognition is distinct from object processing both in terms of behavior and neural processing. Functionally, face processing is disrupted by image manipulations including inversion (Yin, 1969) and negation (Galper, 1970) that do not affect object processing in general. Faces also appear to be recognized holistically (Maurer, Le Grand, & Mondloch, 2002), meaning that observers tend to process the entire face pattern as a gestalt, and subsequently have relatively poor access to smaller patterns within the larger image. This functional difference between face and object processing has been demonstrated both via the composite face effect (Young, Hellawell, & Hay, 1987) and the part-whole effect (Tanaka & Farah, 1993), both of which obtain for faces, but not objects. In terms of the neural basis of face processing relative to object processing, multiple face-sensitive responses have been identified using fMRI (Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997) and event-related potentials (Bentin, Allison, Puce, Perez, & McCarthy, 1996).

If face processing is indeed distinct from object processing, a natural question to ask is how selective face-specific processing is. That is, what is the nature of the boundary between faces and other objects, both in terms of behavior and neural responses? Behaviorally, we know that not all faces are recognized equally well, nor are they recognized in the same way. Participants' expertise with face categories, for example, is a key determiner of both how well they recognize and remember faces, and also the manner in which they process faces. The well-known other-race effect is the most prominent example of how expertise affects these aspects of face processing – other-race faces are in general recognized more poorly than own race faces (Malpass & Kravitz, 1969), but are also less susceptible to inversion (Balas & Nelson, 2010) and the composite face effect (Michel, Rossion, Han, Chung, & Caldara, 2006). Neurally, other-race faces also appear to be processed differently than own-race faces. The fusiform face area responds differently to faces based on race (Golby, Gabrieli, Chiao, & Eberhardt, 2001), for example, and multiple face-sensitive ERP components including the N170 (Balas & Nelson, 2010; Ito, Thompson, & Cacioppo, 2004), the P200 (Stahl, Wiese, & Schweinberger, 2008; Stahl, Wiese, & Schweinberger, 2010), and the N250 (Stahl et al., 2010; Tanaka & Pierce, 2009) appear to be sensitive to the race of faces as well. The extent to which face-specific processing is applied to different images is thus not solely

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http://dx.doi.org/10.1016/j.neuropsychologia.2013.05.022

determined by how face-like a pattern is (Moulson, Balas, Nelson, & Sinha, 2011) but is instead a function of how much experience an observer has had with a particular sub-class of faces. Characterizing the interaction between visual experience and face-specific processing thus remains an important means of understanding the boundary between face and object processing.

In the present study, we chose to address this larger issue by comparing face processing across species categories – specifically, human faces and monkey faces. Comparing the recognition of human faces to the recognition of non-human primate faces is particularly interesting for several reasons. First, comparisons between distinct sub-groups of human faces (across races, ages, or gender) can easily be compromised by a failure to adequately characterize the visual experience of study participants. Adult observers' exposure to monkey faces is typically much more limited, especially with regard to individuation cues which are known to be crucial for maintaining face recognition skills (Scott & Monesson, 2010). Second, though non-human primate faces are not as phylogenetically distant from our own as other species (Taubert, 2009), their facial geometry is nonetheless quite different from the typical 2nd-order arrangement of human features, and surface reflectance properties also differ from human norms considerably. Both of these points suggest that other-species comparisons offer an opportunity to examine large effects of experience on face perception – the combination of limited environmental contact and highly distinct appearance should lead to larger differences between own- and other-species face recognition than are typically observed for within-species comparisons between age groups, sexes, or races. Third, substantial differences in observer experience notwithstanding, several studies have recently demonstrated that multiple aspects of human face processing appear to generalize to a subset of non-human primate faces as well. Behavioral indices of face-specific mechanisms including the inversion effect, effects of facial configuration on recognition, contrast negation, and holistic processing are all manifest in non-human primate faces, suggesting that these faces are to some extent as "special" as human faces (Taubert, 2009). The generality of face-specific mechanisms across species categories does not seem to be complete, however, since other aspects of face-specific processing, including the left-side bias in human face perception (Gilbert & Bakan, 1973) do not obtain robustly in other-species faces (Balas & Moulson, 2011). The nature of the functional boundary between own- and other-species faces, specifically non-human primates, is thus an intriguing and important test case for theories describing how experience affects quantitative and qualitative aspects of mature face processing.

Finally, face-sensitive ERP components are known to respond differentially to own- and other-species faces. In infancy, the putative analog of the adult N170 component shows sensitivity to the species of face images, but inversion only appears to affect this component for human faces (de Haan, Pascalis, & Johnson, 2002). Differential processing of upright and inverted monkey faces does obtain at a later component, the P400, suggesting that continued visual processing of other-species faces by the infant visual system leads to orientation-specific effects on own- and other-species faces. The adult N170 exhibits a more limited selectivity for human vs. non-human primate faces, however. In some cases, the N170 latency does appear to be modestly sensitive to the species of upright faces (Carmel & Bentin, 2002; Wiese, Stahl, & Schweinberger, 2009), but in general the amplitude of the N170 does not differ as a function of species (Wiese et al., 2009) even if observers are presented with a diverse group of other-species faces (Rousselet, Mace, & Fabre-Thorpe, 2004). However, the well-known effect of inversion on the N170 component does display some intriguing species selectivity in adults – in general, the inversion effect (particularly as indexed by the delayed latency of the N170) is stronger for human faces (Rousselet et al., 2004; Wiese et al., 2009), suggesting that whatever aspects of face processing lead to differential processing of faces based on planar orientation are less evident for non-human primate faces at this component. We conclude, therefore, that these species-specific properties of the N170 with regard to upright and inverted faces suggest that similar indices of face-specific processing should also be more evident in human faces than other-species faces.

In the current study, we use contrast-negation as a means to examine the species-specificity of face processing. Contrast negation is known to disrupt face recognition (Galper, 1970) but not object recognition in general (Niederhouser et al., 2007; Vuong, Peissig, Harrison, & Tarr, 2005). Though contrast negation appears to exert some influence on face perception via impairments of shape-from-shading (Kemp, Pike, White, & Musselman, 1996) and the estimation of geometric descriptors of appearance (Kemp, McManus, & Pigott, 1990; Nederhouser, Yue, Mangini, & Biederman, 2007), recent results suggest that the disruption of natural pigmentation is a key factor in the observed effects of polarity reversals on face processing (Russell, 2003; Russell, Sinha, Biederman, & Nederhouser, 2006). Compared to other manipulations of facial appearance, contrast negation is also interesting since it preserves the overall spatial layout of edges in the face image (the *isophotes* of the image (Fleming & Bulthoff, 2005)), but reverses the polarity of shadows and specularities, both of which are cues to 3D shape (Fleming, Dror, & Adelson, 2003; Fleming, Torralba, & Adelson, 2004) and the latter of which is an important cue for processing material properties. Furthermore, full negation of the face can be further broken down into negation of the luminance channel only or negation of hue (Kemp et al., 1990, 1996), in an attempt to dissociate shape-based information (primarily in the luminance channel) from pigmentation-based information (primarily in the hue channel). This dissociation is imperfect and incomplete, especially when applied to 2D images rather than 3D models of individual faces, but nonetheless can yield important insights into how distinct visual features contribute to face recognition processes. Contrast negation is also known to have predictable effects on face-sensitive neural responses that are similar to the effects of face inversion (Itier & Taylor, 2002; Itier, Latinus, & Taylor, 2006). Contrast negation is thus a useful method for determining the extent to which behavioral and neural responses to faces are specialized for the typical appearance of the face.

We designed two experiments to characterize how luminance- and hue-negation interact with face species. In Experiment 1, we asked adult participants to perform a face discrimination task using images of human and monkey faces that were displayed either in positive contrast, or with luminance negation, hue negation, or full contrast negation applied. In Experiment 2, we used the same images to measure participants' responses to original and contrast-negated versions of human and monkey faces while performing a simple go/no-go task. In both cases, we expected that contrast negation would disrupt human face processing more than monkey face processing. Our results indicate however, that contrast negation has qualitatively and quantitatively similar effects across species in terms of discrimination ability, but that the effects of negation on face-sensitive neural responses are manifest at different stages of face processing as a function of species.

2. Experiment 1

In this experiment, we measured adults' ability to discriminate between human monkey faces subject to polarity reversals of luminance information, hue information, or both. In general, these manipulations should substantially disrupt face processing, especially for human faces.

2.1. Methods

2.1.1. Subjects

We recruited 24 adults (12 female) between the ages of 18–22 years old (mean age=20 years, 3 months) to participate in this experiment. All participants reported normal or corrected-to-normal vision, and no history of visual or neurological impairment. All participants were naïve to the purpose of the study and had not been exposed to the experimental stimuli prior to their participation.

2.1.2. Stimuli

We used 12 full-color photographs of adult men and 12 photographs of macaque monkeys for this task. Both sets of faces were cropped with an oval window to remove external face features including the ears, hairline, and jaw. Face size was matched as closely as possible across species (human faces were 256×256 pixels, while monkeys were 300×256 pixels) given the differing aspect ratios of the faces as depicted in our raw images.

Contrast polarity was manipulated in the GIMP image editing application. We carried out full negation of the face (simultaneous luminance and hue negation) by inverting pixel values across the entire image. We negated the hue channel selectively by re-coloring our stimuli with a 180-degree rotation of the hue values in HSV space. We negated the luminance channel selectively by applying full negation to the entire image, and then rotating hue values back to the original values. Examples of all 4 versions of the stimuli for each species category are depicted in Fig. 1.

2.1.3. Procedure

We asked participants to complete a 4AFC oddball detection task that required them to discriminate between human and monkey faces subject to the manipulations of luminance and hue polarity described above. On each trial, we presented participants with an array of 4 faces arranged in a cross around the center of the display (Fig. 2). Three of these faces were identical and served as distractors. The remaining "oddball" face was the target image. Participants were asked to identify the location of the target image on each trial as quickly as possible by touching it.

Participants viewed the stimuli from a distance of approximately 50 cm, which was controlled using a chin rest. At this distance, each individual face subtended approximately 1.75° of visual angle. Participants had unlimited time to view each stimulus array, but were encouraged to respond as quickly and accurately as possible. Stimuli were displayed and responses were recorded using an ELO Touchscreen that displayed the images at a resolution of 1024×768. All stimulus display and response collection routines were controlled by custom software written using the Psychtoolbox extensions for Matlab (Brainard, 1997; Pelli, 1997).

Participants completed 4 blocks of trials in Experiment 1, with contrast polarity varied across blocks and species randomized within each block. We chose to vary contrast polarity across blocks so that observers were not subject to random (and extreme) changes in stimulus appearance from trial to trial – a blocked design minimizes the contribution of task-switching costs, etc. to any negation effects we might observe. Each block was comprised of 96 trials (48 human arrays and 48 monkey arrays) and block order was counterbalanced across participants. Participants typically completed the experiment in 20–30 min.

3. Results

3.1. Accuracy

Participants achieved very high accuracy in all conditions. Performance was greater than 95% for human and monkey faces in all cases, which is not unexpected given that observers had unlimited time to locate the target face and also that the distractors on each trial were identical. With accuracy levels so close to ceiling, we did not choose to analyze the accuracy data further.

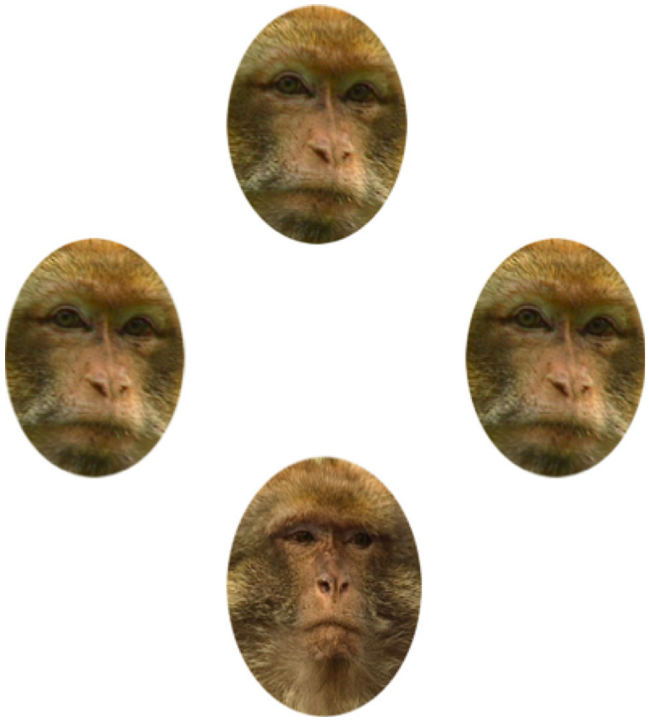


Fig. 2. A schematic view of the arrangement of faces on a single trial in Experiment 1. The target image in this array is the bottom face, which differs from the three identical distractors positioned at the other locations. Participants were asked to indicate the location of the target by touching it as quickly as possible.



Fig. 1. Examples of original human and monkey faces (upper left corner of each panel), luminance-negated stimuli (upper right), hue-negated stimuli (lower left), and full contrast negation (lower right).

3.2. Response times

We analyzed the average response time to correctly locate the target face in all conditions using the median RT. Response time data typically has substantial skew and the median is more robust to outliers than other measures of central tendency.

These RT values were analyzed using a $2 \times 2 \times 2$ repeated-measures ANOVA, with face species (human/monkey), luminance polarity (positive/negative), and hue polarity (positive/negative) as within-subject factors. The median response time averaged across participants within each condition is displayed in Fig. 3.

The ANOVA revealed main effects of species ($F(1,23)=60.7$, $p<0.001$), luminance polarity ($F(1,23)=36.0$, $p<0.001$), and hue polarity ($F(1,23)=25.1$, $p<0.001$). Participants made correct responses more quickly to monkey faces than human faces, and were faster to correctly locate the target for positive luminance and hue polarity. We also observed a significant interaction between luminance and chroma ($F(1,23)=5.23$, $p<0.05$). Post-hoc tests revealed that this interaction was driven by significantly faster response times between RTs measured in the positive luminance and positive hue condition and all other conditions – paired comparisons between the positive hue and positive luminance conditions and all other conditions reached significance after correction for multiple comparisons ($p<0.002$ in all cases following a paired-samples t-test), but no other comparisons reached the corrected significance level. We therefore conclude that the interaction results from RTs that are substantially faster when the faces are presented in their natural polarity compared to all other conditions.

4. Discussion

The data from Experiment 1 reveal that contrast negation affects human faces and monkey faces in the same way – while overall performance with monkey faces is better, negating luminance and color each impacts performance, but the negation of both is sub-additive. Our results are broadly consistent with Parr & Taubert's (2010) result demonstrating that contrast negation of non-human primate faces impairs face discrimination in non-human primates. In our task (as in theirs) the negation of monkey faces removes information that is useful for discrimination. Our results do differ from previous studies in which both luminance and color negation were employed however. We find, contrary to Kemp et al. (1996), that color negation and luminance negation lead to similar discrimination costs. This could be due to differences in task demands. Our discrimination task required participants to discriminate between two real faces, rather than detect changes in eye spacing, etc. It is possible that detecting subtle changes in face geometry is indeed more reliant on information in the luminance channel specifically, or perhaps the absence of the bounding contour in our study forced participants to make more use of the surface-based cues in the interior region of the face.

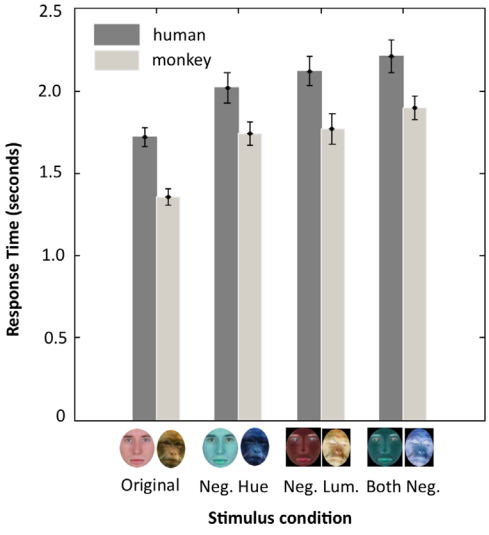


Fig. 3. The median response time averaged across participants for all experimental conditions in Experiment 1. The error bars represent ± 1 standard error of the mean.

With regard to the selectivity of face processing for faces of other species, our data further indicate that the faces of non-human primates may be processed more like human faces than like generic objects. Negation effects obtain weakly for objects like greebles (Vuong et al., 2005) and smooth blobs (Niederhouser et al., 2007), but do obtain in our first task for monkey faces. This suggests that similar to human faces, non-human primate faces are also encoded in a manner that uses local polarity relationships as well as the spatial layout of edges in the image. This is in good accord with results that suggest that other markers of face-specific processing, including the composite face effect and the inversion effect are evident both when humans view non-human primate faces (Taubert, 2009) and when non-human primates are the observers (Parr, 2010). Our main effect of species favoring faster identification of the target for monkey faces is unexpected, but most likely simply a by-product of objectively different physical differences in appearance between the two stimulus sets. A strict perceptual expertise account would certainly predict that monkey faces should be recognized more slowly and less accurately than human faces, but the low-level properties of the stimulus set may easily overcome this predisposition, especially in an image-level discrimination task like the one we posed to our participants. Thus, we do not suggest that the main effect of species reflects specialization of the human visual system for monkey faces – rather, we suggest that the more interesting conclusion to be drawn from this data is that the impact of luminance and hue polarity does not appear to be manifest in a species-specific manner.

We continued by examining the neural selectivity of face-sensitive responses for positive and negative contrast images of human and monkey faces. We used event-related potentials to measure the responses of the N170 (Bentin et al., 1996) and the P200 components, both of which have been shown to be sensitive to whether faces belong to an in-group or an out-group as defined by observer experience (Balas & Nelson, 2010; Stahl et al., 2008). If the processes underlying these components are indeed selective for faces based on expertise, we predicted that contrast negation effects may be differentially evident as a function of species category. Specifically, we predicted that contrast negation effects would obtain for human faces, but not monkey faces (our behavioral data from Experiment 1 notwithstanding). The logic behind this prediction is that ERPs are: (1) potentially more sensitive than behavioral measures and (2) capable of revealing neural dissociations that are difficult or impossible to measure behaviorally. Thus, though human and monkey faces may appear equally "special" with regard to contrast negation as defined by behavioral measures, they may differ substantially with regard to the underlying neural processes that support their discrimination from one another.

5. Experiment 2

In this experiment, we measured participants' neural responses to human and monkey faces subject to the same manipulations of luminance and hue polarity that we implemented in Experiment 1. We used event-related potentials (ERPs) to characterize face-sensitive neural processing by examining two components, the

N170 and P200, which have been implicated in different stages of face processing and both display sensitivity to the race/species category of faces. Additionally, and to extend the results of previous studies, we include an analysis of the P100 component to assess the extent to which lower-level visual processing of own- and other-species faces of varying contrast polarity predicts the responses at the N170. The previous studies (Rousselet et al., 2004) have not included an analysis of this component (but see Wiese et al. (2009) for a footnote describing their P1 data), making it difficult to estimate the contribution of low-level stimulus differences to the observed effects at later components.

5.1. Methods

5.1.1. Subjects

We recruited 22 adults (12 female) between the ages of 19 and 32 (mean age: 21 years, 1 month) to participate in this study. None of these participants had taken part in Experiment 1, and all participants were naïve as to the purpose of the study. All participants reported normal or corrected-to-normal vision and had no history of visual or neurological disorders. We assessed handedness using the Edinburgh Handedness Inventory and only included right-handed participants in the task.

5.1.2. Stimuli

We used a subset of the images of human and monkey faces described in Experiment 1. We removed 6 monkey images from the original stimulus set to exclude macaque faces that were outliers in terms of appearance relative to the rest of the set – these images had visible color artifacts that were readily apparent on the display used for EEG testing. These were removed from the stimulus set to minimize the contribution of low-level image artifacts to ERP variability. We also removed 6 human images to balance the number of stimuli in each category. In neither case do these subsets of images appear to contribute disproportionately to the effects observed in Experiment 1. A repeated-measures ANOVA applied to the median RT from trials in Experiment 1 that contained this subset of images yielded qualitatively the same pattern of results: Main effects of species ($F(1,23)=38.8$, $p<0.001$), luminance polarity ($F(1,23)=54.8$, $p<0.001$), and hue polarity ($F(1,23)=21.6$, $p<0.001$), as well as the interaction between luminance and hue polarity we obtained in the full task ($F(1,23)=6.00$, $p=0.022$). Additionally, a set of cartoon images were used as "oddball" images for the go/no-go paradigm we implemented in this experiment.

5.1.3. Procedure

Following application of the sensor net, participants sat in a sound-isolated, darkened room approximately 50 cm away from the display. We presented stimulus images to our participants using custom routines written in EPrime v2.0. On an individual trial, a single image was presented on a medium-gray background for 500 ms. Participants were asked to press a large plastic button if the image was one of a pre-defined set of oddball images shown to them prior to net application, and to refrain from pressing the button in all other instances. Images were presented at their native size (described in Experiment 1), and each image presentation was followed by an inter-stimulus interval of variable duration (drawn at random from a uniform distribution spanning 800–1500 ms).

We presented participants with 48 images per condition (8 repetitions of 6 unique faces per species) of the human and monkey faces rendered with all combinations of positive and negative luminance and hue polarity. Participants also viewed 32 instances of oddball images for a grand total of 416 trials. Image order was fully randomized and participants completed the experimental session in a single block of trials.

5.1.4. 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. Prior to the start of each experimental session, we checked impedances online and only began the experiment after establishing stable impedances below a threshold of 100 kΩ.

After the conclusion of the experimental session, we processed each subject's continuous EEG data using NetStation v4.3.1 (Eugene, OR). We applied a 30-Hz lowpass filter and segmented individual trials using stimulus onset to define a 100 ms pre-stimulus baseline period and a 900 ms post-onset window, yielding a 1000 ms segment for each trial. We baseline-corrected these segments by subtracting the average voltage measured in the baseline period from the entire segment and following this, we hand-edited the segmented data for EOG and motion artifact. We rejected data from any individual sensors that had lost contact, and rejected entire segments if there was evidence of wide-spread drift, eye movements or eye blinks, or more than 7 rejected sensors. We used spherical spline interpolation to replace the data from rejected sensors, and subsequent to this, we computed individual subject averages for each experimental condition. Finally we re-referenced the data from each subject to an average reference. We rejected the data from 3 subjects on the basis of too few usable segments within some experimental conditions (<25 of 48 trials), leaving us with a total of 19 participants in our final sample.

6. Results

We were able to identify a clear N170 over occipito-temporal electrodes using the grand average calculated across all participants. We selected a total of eight electrodes (four per hemisphere) as the basis for our analysis of the N170 and P200 based on previous reports and visual inspection of the grand average waveforms. We chose to analyze the N170 within a time window of 160–220 ms post-stimulus onset and analyzed the P200 within a time window of 220–300 ms. Additionally, we measured the P1 component within a time window of 100–160 ms so that we could examine the responses at the N170 in comparison to the presumably low-level effects observed at the P1. Within each time window, we calculated the peak amplitude for each condition,

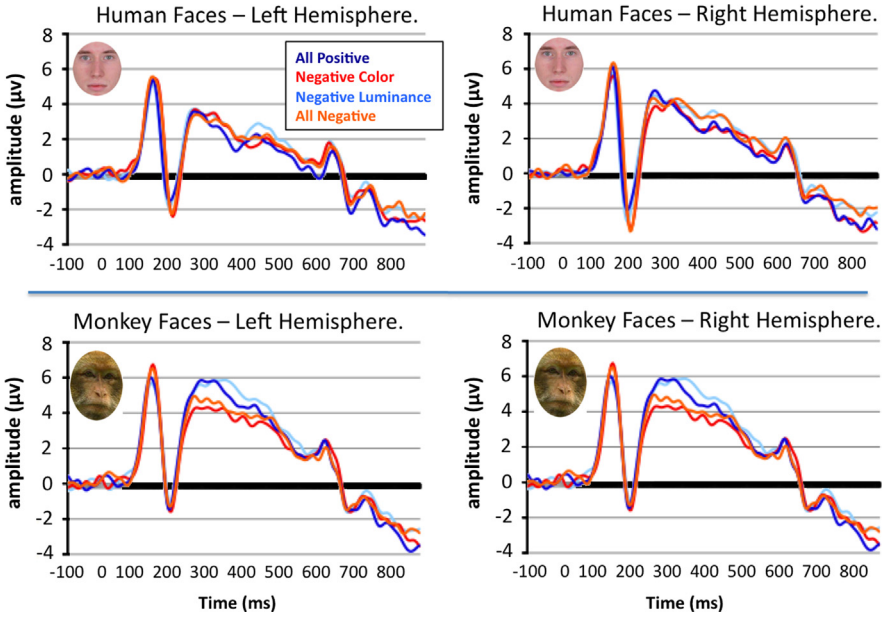


Fig. 4. Average ERP waveforms for all stimulus conditions measured in the left and right hemispheres.

averaged across the electrode group within each hemisphere. We calculated the latency of the N170 and P1 using latency-to-peak, the outcome of which we confirmed manually for each participant to ensure that spurious latency values were not computed based on artifacts of window width or local noise. In Fig. 4, we display average ERPs for each condition, averaged across the sensors within right and left hemisphere groups separately.

6.1. P1 – peak amplitude

We analyzed the peak amplitude of the P1 in each experimental condition using a $2 \times 2 \times 2 \times 2$ repeated-measures ANOVA with species (human/monkey), luminance polarity (positive/negative), hue polarity (positive/negative) and hemisphere (left/right) as within-subjects variables. This analysis yielded only a three-way interaction between species, hue polarity, and hemisphere ($F(1,17)=4.383$, $\eta^2=0.216$, $p=0.039$) such that monkey faces exhibited a larger effect of hue polarity than human faces over left hemisphere electrodes and human faces exhibited a larger effect of hue polarity over right hemisphere electrodes.

6.2. P100 latency

We next analyzed the latency to peak for the P100 component using a repeated-measures ANOVA with the same factors described above. This analysis revealed only an interaction between species and hemisphere ($F(1,17)=4.44$, $\eta^2=0.198$, $p=0.049$), such that we observed a significant hemispheric difference for monkey faces (paired-sample t-test, $p<0.05$) but not for human faces. Critically, neither of the effects of luminance polarity ($F(1,17)=1.73$, $p=0.20$) nor hue polarity ($F(1,17)=3.76$, $p=0.07$) reached significance, nor did these factors interact with species category ($F<1$ in both cases).

6.3. N170 – peak amplitude

We analyzed the peak amplitude of the N170 in each experimental condition using a repeated-measures ANOVA with the same within-subjects factors as described above. This revealed a main effect of species ($F(1,17)=17.1$, $\eta^2=0.487$, $p<0.001$) such that human faces elicited a more negative response than monkey faces. We also observed a main effect of hue polarity ($F(1,17)=4.74$, $\eta^2=0.208$, $p=0.043$) such that negated hue led to a more negative peak. Finally, we also observed a three-way interaction between species, luminance polarity, and hemisphere ($F(1,17)=5.012$, $\eta^2=0.218$, $p=0.038$). Post-hoc tests revealed that this interaction was driven by a significant hemispheric difference (larger right hemisphere peaks) for positive polarity human faces (paired-samples t-test, $p<0.05$) but a significant hemispheric difference for negative polarity monkey faces ($p<0.05$). In each case, the hemispheric differences for the alternate polarity conditions did not reach significance. No other main effects or interactions reached significance ($F<1$ in all cases).

6.4. N170 – latency to peak

We continued by analyzing the latency to the peak of the N170 component in each of our experimental conditions. As described above, we submitted the latency values for all conditions to a $2 \times 2 \times 2 \times 2$ repeated-measures ANOVA with species, luminance polarity, hue polarity and hemisphere as within-subject factors.

We observed a main effect of hue polarity ($F(1,17)=18.7$, $\eta^2=0.51$, $p<0.001$) due to faster latencies in response to positive hue images ($M=185$ ms, s.e.m.$=2$) than to negative hue images ($M=189$ ms, s.e.m.$=1.7$). Critically, we also observed an interaction between hue polarity and species ($F(1,17)=11.1$, $\eta^2=0.38$, $p=0.004$), such that the effect of hue polarity was not evident for monkey faces ($M_{\text{positive-hue}}=187$ ms, $M_{\text{negative-hue}}=188$ ms) but was significant for human faces ($M_{\text{positive-hue}}=184$ ms, $M_{\text{negative-hue}}=190$ ms). This interaction indicates that the sensitivity of the N170 latency to hue-negated faces is species-specific. Finally, we also observed a three-way interaction between hue polarity, species, and hemisphere ($F(1,17)=5.0$, $\eta^2=0.22$, $p=0.03$). Similar to the 3-way interaction observed for peak amplitude, post-hoc tests revealed that this interaction was also driven by a significant hemispheric difference (faster peak latencies in the right hemisphere) for positive hue polarity human faces (paired-samples t-test, $p<0.05$) while a significant hemispheric difference for negative hue polarity monkey faces obtained ($p<0.05$). As in the previous data, the hemispheric differences for the alternate polarity conditions did not reach significance. No other main effects or interactions reached significance.

6.5. P200 – peak amplitude

We continued by analyzing the mean amplitude of the P200 response, submitting the peak amplitude measured over the aforementioned time window to a repeated-measures ANOVA with the same factors as described above. We observed a main effect of species ($F(1,18)=9.75$, $\eta^2=0.35$, $p=0.006$) such that monkey faces elicited a larger peak amplitude. We also observed a main effect of hue polarity ($F(1,18)=11.61$, $\eta^2=0.39$, $p=0.003$), such that negative hue polarity lead to a smaller peak amplitude. Finally, we also observed a significant interaction between species category and hue polarity ($F(1,18)=6.74$, $\eta^2=0.27$, $p=0.018$), such that the negation effect for monkey faces ($M_{\text{positive-hue}}=7.10$ μV, $M_{\text{negative-hue}}=6.02$ μV) was larger than for human faces ($M_{\text{positive-hue}}=5.64$ μV, $M_{\text{negative-hue}}=5.46$ μV). This interaction suggests a species-specific effect of hue polarity, but in contrast to the results we observed at the N170, it is hue negation of monkey faces that affects the magnitude of the response. No other main effects or interactions reached significance.

6.6. P200 – latency to peak

Finally, we also examined the P200 latency to peak amplitude using an ANOVA with the same factors described for our previous analyses. This revealed a main effect of hemisphere ($F(1,18)=4.52$, $\eta^2=0.20$, $p=0.048$) favoring longer latencies in the right hemisphere. We also observed an interaction between luminance polarity and hue polarity ($F(1,18)=5.56$, $\eta^2=0.24$, $p=0.030$), such that the effect of hue polarity was larger when luminance polarity was positive. Finally, we observed an interaction between hemisphere and luminance polarity ($F(1,18)=6.46$, $\eta^2=0.26$, $p=0.021$), such that the effect of hemisphere was only evident when images were presented with positive luminance polarity. We note that none of these effects depended upon species category, and no other main effects or interactions reached significance.

7. General discussion

Our data from Experiment 2 demonstrate that hue negation affects the latency of the N170 component (as well as its peak amplitude) – the response to human faces is modulated by negation in a manner consistent with previous results (Itier & Taylor, 2002; Itier et al., 2006). This sensitivity is dependent on stimulus category, however, in a manner that is not predicted by the responses at the P100: specifically, the N170 latency to monkey faces is not affected by the reversal of hue information, even though our behavioral results from Experiment 1 indicated that this manipulation did impact face discrimination for human

and monkey faces in the same way. Critically, we did not observe this latency effect at the P1, suggesting that this latency effect is not the result of low-level differences in the stimuli carrying over from a previous stage of processing. We conclude therefore, that the N170 latency is apparently sensitive to hue polarity in a species-specific manner.

Similar species-specificity has been found for the face inversion effect observed at the N170 (Itier, Van Roon, & Alain, 2011), despite a robust inversion effect for monkey faces behaviorally (Taubert, 2009). This suggests that in general, image manipulations that do disrupt behavioral performance with own- and other-species faces do not necessarily disrupt neural responses in the same manner. These critical features of our data also preclude an explanation based solely on inter-stimulus similarity (Thierry, Martin, Downing, & Pegna, 2007) since this would predict similar effects at the N170 based on the similar discrimination effects observed behaviorally (though other aspects of our data may be impacted by such factors).

We also observed a species-specific negation effect at later stages of visual processing, as reflected in our results obtained by analyzing the peak amplitude of the P200, revealing that monkey faces are impacted by hue negation more than human faces at later stages of processing. This effect reveals that it is too simplistic to conclude that species-specific processing is limited to the face category of expertise. Elsewhere, we observed either main effects of contrast polarity, or selective effects on the processing of human faces, but not monkey faces. The results from the P200 provide intriguing evidence that at some stages of processing we may find selective effects on the processing of other-group faces. We conclude that contrast negation affects both species (consistent with Experiment 1) at different stages of face processing, and that the impact of contrast reversal may be realized in different species-specific ways for each face category.

There are some important discrepancies between our current data and some previous results, however. First, we have observed a larger negative response at the N170 for human faces relative to monkey faces, differing from several previous results (Carmel & Bentin, 2002; Wiese et al., 2009) that report no difference in the N170 amplitude as a function of species category. We note, however, that our otherwise counter-intuitive result favoring a smaller N170 for monkey faces is to some extent consistent with the observed effects in Experiment 1, in which we found that monkey faces were more quickly discriminated than human faces. As we suggested in the discussion of those results, we believe that this reflects low-level differences in appearance variability between our species categories. The monkey faces we selected may simply be more different from one another than the human faces we selected – in the absence of a robust computational estimate of image dissimilarity we are of course speculating about the objective differences between the faces, but we suggest that our data is largely consistent with this interpretation. If this is the case, and the data from Experiment 1 suggest that it is, our monkey faces are objectively more dissimilar to one another than our human faces, potentially leading to a smaller N170 amplitude by virtue of increased trial-to-trial variability (Thierry et al., 2007). This does not suggest that the human visual system is somehow tuned to monkey faces, but rather that the physical differences between the stimuli contribute to the magnitude of the N170. We note that inter-stimulus variation is not the sole factor that drives category-selective responses (Rossion & Jacques, 2008), but that it does play a role in waveform measurement. We also observe a larger response to monkey faces at the P200. With regard to own-race and other-race faces, results describing effects at the P200 are mixed, due at least in part to variability in how different groups have identified the P200. In many cases where the P200 has been reported to be larger for other-group faces (Ito & Urland, 2003, 2005), this effect may actually be attributed to the Vertex Positive Potential (or VPP) rather than the P200 per se. The VPP is typically observed over more central sites and has an early onset that reflects the fact that it is the positive counterpart to the N170 (Joyce & Rossion, 2005). As such, the effects reported by Ito and Urland (2003, 2005), among others, can reasonably interpreted as manifestations of a larger response to other-race faces at the N170 (Wiese, 2012). In cases where the occipital–temporal P200 has been analyzed for sensitivity to own-race and other-race faces, larger responses to own-race faces are evident (Stahl et al., 2008, 2010) and similar results obtain for comparison of own-age and other-age faces (Wiese, 2012; Wiese, Komes, & Schweinberger, 2012). Our analysis of the occipito-temporal P200 differs from these latter results. Again, we suggest that the main effect of species that we observed may have more to do with trial-to-trial variability due to appearance variation within each species rather than higher-level processing. However, in both cases, we suggest that these main effects of species, which are consistent with our behavioral data from Experiment 1, are less important than the interactions we observe between species and hue polarity both at the N170 and the occipito-temporal P200.

How do the results we observe at the P200 fit into an expertise-based account of own- and other-species processing? If later stages of visual processing primarily reflect the extent to which a particular face pattern is seen as “other” vs. “own,” why should contrast-negated human faces not also modulate the amplitude of later responses? One possible account is that the P200 (and other advanced stages of face processing) plays a role in combining the parts of a face into a larger gestalt (Milivojevic, Clapp, Johnson, & Corballis, 2003), and that the negated monkey faces are the least holistically-perceived stimuli among the images we included in this study. Should this be the case, we would expect to find a similar species x contrast-polarity interaction in a composite face task using both positive and negative faces of both species, a manipulation which to our knowledge has not been carried out.

Our data provide converging support for a description of human face processing that includes the faces of non-human primates within the set of patterns that are processed differently than generic objects, but also raise several important issues. For example, how general is the behavioral contrast negation effect? Unlike recent studies of the inversion effect (Itier et al., 2011) we have only included one non-human category of faces in our study. Based on the pattern of data observed for stimulus inversion, we would predict that faces more phylogenetically distant from our own, including sheep, dogs, and cats, should exhibit a markedly less pronounced negation effect. Similarly, how general are the effects we observe at later stages of processing? Here, we might expect that negated animal faces should in general elicit differential responses at late components, but not earlier. We have also not considered the role of task in the current study, opting instead for a basic zero-back procedure using an easily identifiable oddball. Pre-task training can modulate the effect of race on multiple visual ERP components (Tanaka & Pierce, 2009), and it thus stands to reason that the impact of image negation may be realized differently as a function of task, possibly in a manner that interacts with species. For example, the tacit task associated with viewing monkey faces may be categorization rather than individuation, leading to different responses when the presumptive explicit task is effectively null. Finally, we may also ask how the differential neural processing of human and monkey faces with regard to negation emerges as a function of experience, specifically over a developmental timecourse. Own and other-race faces, for example, are processed differently by 9-month old infants and adults with regard to the use of surface-based vs. shape-based cues (Balas & Nelson, 2010; Balas, Westerlund, Hung, & Nelson, 2011), suggesting that there is an important change in how pigmentation

is used as experience accumulates and ultimately favors one race over the other. Given that contrast negation is a particularly useful tool for understanding how the disruption of pigmentation affects face processing (Russell & Sinha, 2007), a developmental study of the species-specificity of contrast negation would reveal important aspects of how appearance tuning for shape and pigmentation unfolds as a function of real-world expertise.

Acknowledgments

This publication was made possible by ND EPSCoR NSF #EPS-0814442 and COBRE Grant P20 GM103505 from the National Institute of General Medical Sciences, a component of the National Institutes of Health (NIH). Its contents are the sole responsibility of the authors and do not necessarily represent the official views of NIGMS or NIH. Our thanks to Mike Mangini for helpful discussions of the data and an anonymous reviewer for many helpful comments on the previous drafts of the manuscript.

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