



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



Benjamin Balas<sup>a,\*</sup>, Kate Stevenson<sup>b</sup>

<sup>a</sup> Department of Psychology, North Dakota State University, Fargo, ND 58102, USA

<sup>b</sup> Department of Psychology, Concordia College, Moorhead, MN, USA

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### 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 determinant 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

\* Corresponding author. Tel.: +1 701 499 5276; fax: +1 701 231 8426.  
E-mail address: benjamin.balas@ndsu.edu (B. Balas).

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; Niederhouser, 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, & Niederhouser, 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.

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