

The Composite Face Effect in Chimpanzees (*Pan troglodytes*) and Rhesus Monkeys (*Macaca mulatta*)

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The accurate recognition of individuals is a cornerstone of social exchange in primates. Current approaches to the study of individual recognition, however, are focused on human performance and only occasionally reference comparative research for support. A number of studies have suggested that humans can easily recognize thousands of individual faces and that this perceptual expertise is supported by holistic processing, a phenomenon best demonstrated by the composite face effect (CFE). Recent advances have indicated that the CFE in humans is robust to changes in contrast polarity (positive or negative). Here we apply a two alternative forced choice match-to-sample paradigm across two species of nonhuman primate, chimpanzees (*Pan troglodyte*) and rhesus monkeys (*Macaca mulatta*). We find strong evidence that chimpanzees and rhesus monkeys experience interference from holistic processing in the positive contrast condition. While there is some indication that the chimpanzees experienced a CFE in the negative contrast condition, there was no evidence of a CFE in the corresponding rhesus monkey data. These results suggest that, while holistic processing is a general mechanism, rhesus monkeys are more sensitive to contrast-polarity than humans.

Keywords: primate cognition, individual recognition, face processing, match-to-sample

Humans are experts at recognizing the faces of conspecifics. To access identity-specific information, it is generally agreed that faces are processed holistically (Bruce et al., 2000; Farah, Wilson, Drain, & Tanaka, 1998; Leder & Carbon, 2006; Richler, Cheung, & Gauthier, 2011; Sergent, 1984; Thompson, 1980; Young, Hellawell, & Hay, 1987). This is taken to mean that facial features are involuntarily integrated to create a single unit of analysis (Davidoff & Donnelly, 1990; Leder & Carbon, 2005; Tanaka & Farah, 1993). In recent years the composite face effect (CFE) has emerged a compelling behavioral marker of holistic processing (Maurer, Le Grand, & Mondloch, 2002; McKone, Kanwisher, & Duchaine, 2007). The CFE has attracted a lot of attention because it does not occur for nonface objects (for a recent review see McKone & Robbins, 2011; for an opposing view see Gauthier & Tarr, 2002). The implication is that CFE reflects a processing style that is unique to faces.

Subjects in the seminal investigation of the CFE were asked by Young et al. (1987) to either name the top half or bottom half of a face. It was reported that pairing two different half-faces together slowed the naming of a familiar half-face when the halves were

aligned. Performance recovered when the two halves were framed shifted so that they were no longer aligned (Young et al., 1987; also see Goffaux & Rossion, 2006; Hole, 1994; Hole, George, & Dunsmore, 1999; Rossion & Boremanse, 2008). This advantage for misaligned trials over aligned trials (the CFE) has been taken as strong evidence that people perceive and recognize faces as perceptual wholes, rather than collections of independent features.

In humans, the CFE has been investigated extensively with behavioral (Carey & Diamond, 1994; Goffaux & Rossion, 2006; Hole, 1994; Hole et al., 1999; Le Grand, et al., 2006; Rossion & Boremanse, 2008; Young et al., 1987) and neurological (Freiwald, Tsao, & Livingstone, 2009; Jacques & Rossion, 2006; Kuefner, de Heering, Jacques, Palmero-Soler, & Rossion, 2010; Schiltz, Dricot, Goebel, & Rossion, 2010) techniques. In contrast to the many studies that have examined the CFE in humans, little has been done to test holistic processing using the CFE in nonhuman primates.

Studies of holistic face processing in nonhuman primate species have relied almost exclusively on the face inversion effect (FIE). There have been numerous demonstrations that both chimpanzees (Parr, Dove, Hopkins, 1998; Parr & Heintz, 2006; Tomonaga, 2007) and macaque monkeys (Dahl, Wallraven, Bulthoff, & Logothetis, 2009; Gothard, Brooks, & Peterson, 2009; Parr, Heintz, & Pradhan, 2008; Vermeire & Hamilton, 1998) find faces harder to discriminate when they are turned upside. However, all of these studies suffer from the same constraint; that the FIE only shares an indirect relationship with holistic processing (McKone et al., 2007; Rossion, 2008, 2009). To date, there have only been three studies that have attempted to measure the CFE in nonhuman primates (Dahl, Logothetis, & Hoffman, 2007; Parr, Heintz, & Akamagwuna, 2006; Taubert & Parr, 2009; see Parr, 2011 for a review).

Parr, Heintz, and Akamagwuna (2006) reported a composite effect for conspecific (but not human) faces in chimpanzees.

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Having adopted a standard match-to-sample procedure, every trial presented a subject with a sample face, comprised of two halves that were drawn from different individuals. The subjects were required to select the matching face from two choices, the identity of the top half-face or the identity of the bottom half-face. As there was no incorrect answer, there was no differential reinforcement and the dependent variable was the number of times the subjects chose to match the features in the top half of the face. Parr et al. reported that the subjects selected the top half more frequently in the aligned condition compared to the misaligned condition. However, it remains unclear whether that chimpanzees experience the CFE because it is possible to expect this result without inducing holistic processing. For example, a spontaneous response bias dependent on the alignment of the sample (i.e., match the face in the top of the sample in aligned trials and the bottom of the sample in the misaligned trials) would produce the same outcome.

A study of rhesus monkeys reported systematic changes in eye movements dependent on whether features were presented in the aligned or misaligned format (Dahl et al., 2007). Despite its intuitive appeal, this finding is at odds with available human data that suggests that the CFE operates independent of fixations (de

Heering, Rossion, Turati, & Simion, 2008). A more recent investigation of the CFE in rhesus monkeys used a match-to-sample procedure and found evidence consistent with holistic interference when rhesus monkeys were tested with chimpanzee faces. However, this study was limited in its overall conclusion because it failed to include a conspecific face condition (Taubert & Parr, 2009). The primary goal of this current study was, therefore, to test and directly compare the performance of chimpanzees and rhesus monkeys using the same experimental procedure.

We adopted a standard simultaneous two alternative forced choice match-to-sample (MTS) procedure because our subjects had many years matching complex objects, including faces, in this context. Also, the MTS procedure was ideal for this study because it allowed us to measure the subject's ability to perform a face-matching task while ignoring task irrelevant information in the bottom half of the faces. Similar to Parr et al. (2006) we included control trials where subjects simply had to match top halves of faces (see Figure 1a). This was necessary because the subjects were not trained with the experimental stimuli or specifically directed to match the information in the top half of the face and we would need some indication of their ability to match half-faces. In

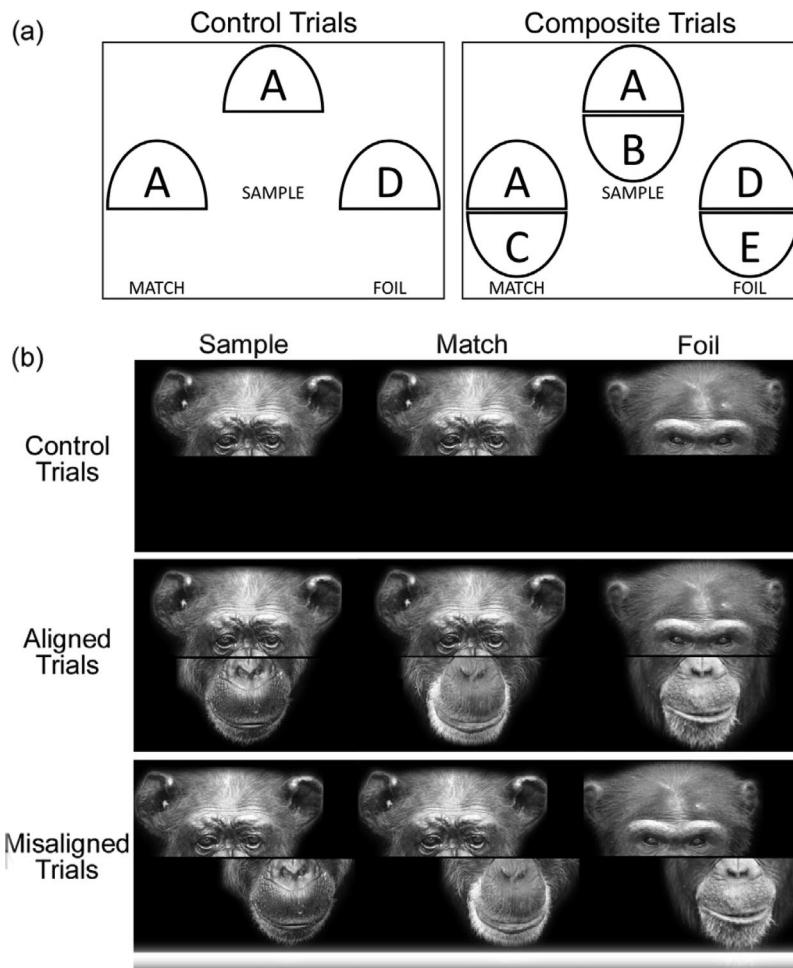


Figure 1. (a) A schematic comparing control trials with composite (aligned and misaligned) trials. (b) Examples of experimental stimuli used in each of the trial formats (control, aligned, and misaligned).

the composite trials, the only matching information was in the top half of the sample and the match (i.e., the task was identical in the control and experimental trials; see Figure 1a). According to the holistic hypothesis, matching top halves ought to be easier in the misaligned condition than in the aligned condition because in the aligned condition the identity of matching features would be integrated by holistic processing and perceived as different (see Figure 1b).

In related research, Hole et al. (1999) reported that holistic representations are built for positive and negative contrast faces despite ample evidence that human subjects (Galper, 1970) have difficulty discriminating faces once their contrast is reversed. This dissociation is consistent with models of face processing that posit holistic processing takes place before discrimination at the individual level (Maurer et al., 2002; Taubert & Alais, 2011; Tsao & Livingstone, 2008). Under this view, when we see a photographic negative depicting a face, it undergoes holistic processing and is easily identified as a face, but it is difficult to extract identity-specific information from a face once contrast has been reversed. Evidence of the CFE for contrast-reversed faces therefore implies that holistic processing may serve a functionally distinct role and can be decoupled from the processes that analyze identity (for empirical evidence see Konar, Bennett, & Sekular, 2010; Taubert & Alais, 2011). Although Parr and Taubert have already reported evidence that face discrimination performance in both chimpanzees and rhesus monkeys is also subject to the deleterious effect of contrast-reversal, they did not test whether holistic processing was disrupted by contrast-reversal (Parr & Taubert, 2011). For this reason we also included contrast phase as a factor in this present experiment (see Figure 2).

In this study we tested whether chimpanzees and rhesus monkeys experienced holistic interference in a CFE task using conspecific faces that were presented in both positive and negative contrast. We hypothesized that subjects would more accurate in the misaligned (M) compared to aligned (A) trials (the CFE; Young et al., 1987). Furthermore, assuming basic uniformity across the primate order, we expected to find the advantage for misaligned trials regardless of contrast polarity.

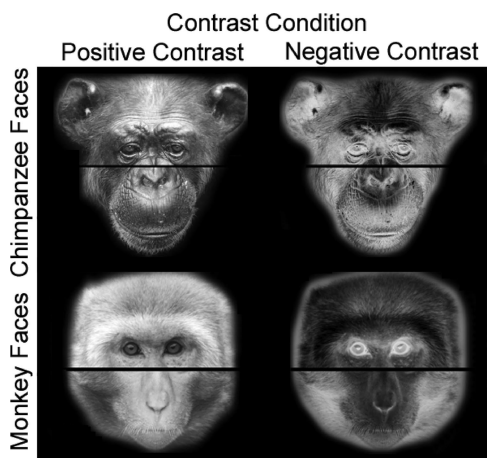


Figure 2. Examples of the experimental stimuli used in each of the contrast conditions (positive and negative).

Method

Subjects

Chimpanzees. Data were collected on five socially housed chimpanzees (*Pan troglodytes*). Three males (Scott, Patrick, and Lamar) and two females (Katrina and Faye). Subjects were between 16 and 22 years old at the time of testing. They were raised in peer groups at the Yerkes Primate Research Nursery until they were four years of age when they were moved to the Yerkes National Primate Research Center (main station, Atlanta, GA). Prior to this experiment, all subjects had received training with matching-to-sample procedures using computerized tasks and the joystick apparatus including several years of experience with face-matching tasks (Parr et al., 1998; Parr & Taubert, 2011; Taubert & Parr, 2011).

Rhesus monkeys. Data were collected from six rhesus monkeys (*Macaca mulatta*). Four were female (Onion, Olive, Chewy, and Lemon), two were male (Rocket and Samosa). All six subjects were between 9 and 10 years old at the time of testing. All were born and raised in large social groups at the Yerkes Primate Research Center field station (Lawrenceville, GA). These rhesus monkeys were relocated to the Yerkes main station (Atlanta, GA) in 2004, at the age of 4 years, where they were pair-housed in a large colony room. Since 2004, all six subjects had participated in several cognitive projects, including a number of face matching experiments (Parr & Heintz, 2008; Parr & Taubert, 2011; Taubert & Parr, 2009).

Visual Stimuli

The stimuli were high-quality digitized photographs of 48 chimpanzees and 48 rhesus monkeys that were prepared in Adobe Photoshop CS5 software. Each chimpanzee face was downsized to a height of 300 pixels (72 dpi) and adjusted for horizontal alignment. The faces were converted to 8-bit grayscale (Positive Contrast) and then copied. The contrast profile of the copied images was then inverted to create the contrast-reversed (Negative Contrast) faces.

The 48 chimpanzee faces were then split into a top and a bottom half at the horizontal midline. Control faces were created by deleting the bottom halves. These were then split into two even groups (24 with positive contrast and 24 with negative contrast). Of the 24 positive contrast faces, 12 would appear as sample/matches with the remaining 12 used as foils. The 24 negative contrast faces were also divided into two groups (12 samples/matches and 12 foils). For Aligned trials, all 48 top halves were paired with nonmatching bottom halves. Positive top halves were paired with positive bottom halves taken from the same stimulus group (samples/matches or foils); negative top halves were paired with negative bottom halves. A gap of approximately five pixels was left between the top and bottom half of all composite stimuli (Aligned and Misaligned faces). Each top half was paired with a different bottom half three times providing a total of 144 recombinants (72 samples/matches and 72 foils). There are illustrative examples provided in Figure 2. The misaligned faces were created from copies of the 144 misaligned faces so that the only difference between aligned and misaligned faces was the position of the bottom half. The bottom half of an aligned face was positioned

directly below the top half whereas the bottom half of a misaligned face was offset by approximately half the width of a face. The rhesus monkey faces were prepared in precisely the same way.

Design and Procedure

Chimpanzee testing took place in the home cage using a mobile testing cart, which housed a 17-inch color monitor covered in clear Plexiglas. During testing, the chimpanzees manipulated a joystick that was mounted on the mesh at the front of the homecage. The presentation of visual stimuli, and the collection of raw data, was controlled by a program created using Visual Basic software.

At the beginning of any given trial, a single image (the sample) would appear in one of four positions: at the center of the top of the screen, at center of the bottom, on the far left, or on the far right. To initialize a trial, the subjects first needed to orient themselves to this sample image using the joystick. Once the cursor had contacted the sample, two comparison images appeared on the opposite side of the screen, equidistant from the sample. Using the joystick to control the cursor, the subjects were required to select one of the two comparison stimuli. One comparison image was the target (the correct choice) while the other image was the foil (the incorrect choice). Following a correct response, the subject was reinforced with a food reward and the following trial would commence after a 2-s interval. An incorrect response resulted in no food reward and a 10-s interval before the next trial.

The task was to match identical top halves (and ignore non-matching top halves). These top halves appeared either in isolation (control trials) or paired with distracting bottom halves (aligned and misaligned trials; see Figure 1a). In aligned and misaligned trials the sample and target were not identical. The only matching information was in the top half of the face. Thus, correct responses required the subjects to ignore the features in the bottom half of the samples.

Stimuli presented as part of the positive contrast condition were grayscale images. There were 72 test trials given in a single positive condition test session (24 half control trials, 24 aligned, and 24 misaligned composite trials). Thus, each of the 12 positive contrast top halves in the sample/match set would appear six times per session, twice in each of the three formats (control, aligned, and misaligned). The composite trials (aligned and misaligned trials) were designed so that sample faces were never identical to the "matching" face. Instead, only features in the top half of the faces matched. The foil was always a completely different face (see Figure 1b). The trials were presented in random order. Each subject completed two test sessions in the Positive Contrast condition (144 trials in total). The negative contrast condition was structured the exact same way, the only difference being the contrast phase of the stimuli. The order that the contrast conditions were completed in was counterbalanced across subjects.

The MTS procedure used to test the rhesus monkeys was generally the same as the procedure for the chimpanzees with a few exceptions that were mostly due to differences in the equipment. Subjects were tested twice daily, once mid morning and once early afternoon. Testing took place in the home cage using a custom-designed testing system, which included two 15-inch touch screen monitors, built into a metal frame, driven by two computers that were transported on a custom-designed testing cart. During testing, a panel was used to separate the rhesus monkeys from their cage

mates and the touch screen monitors were attached to the cage mesh so that each subject could voluntarily respond to the computerized task in their own time. Following a correct response, the subject was reinforced with a food reward via an automated pellet dispenser.

There were 45 test trials given in a single positive condition test session (15 control trials, 15 aligned, and 15 misaligned trials). The trials were presented in random order. Each subject completed four test sessions in the positive contrast condition (180 trials in total). The order of the four sessions was counterbalanced across subjects. The negative contrast condition was structured the exact same way, the only difference being the contrast phase of the stimuli.

Results

Control Trials

The control trials were used to evaluate individual performance for stimuli in their unedited form. For the chimpanzees, the individual criterion was set at 32 or more correct responses based on the binominal distribution for 48 control trials (two-tailed), $p < .05$. The only chimpanzee to score less than 32 was Patrick during the positive condition (see Table 1). As a result Patrick's positive contrast data were removed from further analysis.

The control condition was also used to evaluate the performance of each rhesus monkey. The criterion was set at 39 because if a rhesus monkey was performing at chance in the control condition there was a less than 5% chance they would get 39 or more correct responses (or 21 or fewer correct responses) in 60 trials. As a result of using this criterion, two rhesus monkeys failed the positive condition (Chewy, Lemon) and three failed the negative condition (Rocket, Olive, Chewy; see Table 1).

The Composite Face Effect

For each subject, the number of correct responses in the aligned (A) and misaligned (M) conditions were converted into standardized values (Z scores) for the purposes of comparison. The CFE was calculated by subtracting A from M. As such, positive difference scores reflect holistic face processing. For chimpanzees this was true in the positive and negative contrast condition whereas for the rhesus monkeys it was only true for the positive contrast condition (see Figure 3).

To analyze the results of the positive contrast condition we ran a mixed ANOVA with a 2×2 factorial structure on the normalized data. The between subjects factor was Subject Species (Chimpanzees vs. Rhesus Monkeys). The repeat subjects factor was Alignment (Aligned vs. Misaligned). As predicted by the holistic processing hypothesis, the main effect of Alignment was significant, $F(1, 6) = 55.07$, $p < .01$, partial $\eta^2 = .90$. While there was no evidence that the manipulation of Subject Species influenced performance, $F(1, 6) < 1$, the interaction between Subject Species and Alignment was found to be significant, $F(1, 6) = 7.02$, $p = .04$, partial $\eta^2 = .54$, justifying a series of discrete t tests designed to test the CFE for each Subject Species. The first t test (two-tailed) revealed that the chimpanzees performed better in the Misaligned (M) condition than in the Aligned (A) condition, $t(3) =$

Table 1
A Summary of Individual Performance

Species	Subject	Control	Aligned (A)	Misaligned (M)	CFE (M - A)
Positive contrast condition					
Chimpanzee	Scott	36	31	37	6**
	Katrina	36	33	36	3**
	Patrick	30*	28	30	2**
	Lamar	37	28	34	6**
	Faye	41	26	32	6**
Monkey	Rocket	48	45	48	3**
	Samosa	47	47	49	2**
	Onion	45	41	47	6**
	Olive	43	36	38	2**
	Chewy	38*	41	41	0
Lemon	38*	41	40	-1	
Negative contrast condition					
Chimpanzee	Scott	35	26	32	6**
	Katrina	38	30	31	1**
	Patrick	33	22	23	1**
	Lamar	33	29	32	3**
	Faye	33	21	20	-1
Monkey	Rocket	38*	44	44	0
	Samosa	42	44	41	-3
	Onion	40	42	41	-1
	Olive	37*	41	27	-14
	Chewy	28*	41	32	-9
Lemon	45	40	27	-13	

* Denotes failure to meet criterion. ** Denotes a difference score consistent with a CFE (M - A > 0).

7.01, $p < .01$. The second confirmed the same difference (M > A) in the rhesus monkey data, $t(3) = 3.43, p = .01$. For both tests the alpha level was adjusted for multiple comparisons using the Bonferroni rule ($\alpha = .05/2$).

A second ANOVA with the same structure as the first was run on the negative contrast condition. Counter to prediction, there was no effect of Alignment, $F(1, 6) = .84, p = .39$, partial $\eta^2 = .12$,

nor was there any evidence of an interaction between Subject Species and Alignment, $F(1, 6) = 5.92, p > .05$, partial $\eta^2 = .50$. Overall, there was no evidence that the chimpanzees outperformed the rhesus monkeys, $F(1, 6) < 1$.

Discussion

The aim of this study was to understand the holistic nature of face perception in chimpanzees and rhesus monkeys using a behavioral measure of performance in a CFE task. The experiment revealed composite face effects in the positive contrast condition, suggesting that both chimpanzees and rhesus monkeys process positive faces holistically. This result is consistent with the previous studies that have also reported evidence of holistic face processing in these species, using different dependent measures (Dahl et al., 2007; Parr et al., 2006) or unfamiliar species faces (Taubert & Parr, 2009). This article, therefore, unifies the existing literature by providing strong behavioral evidence that chimpanzees and rhesus monkeys, like humans, experience holistic interference in a CFE task.

The current experiment also tested whether the CFE was tolerant of contrast reversal. The negative contrast condition yielded a weaker result in comparison to the positive contrast condition, nonetheless, we note that the trend in the chimpanzee data was the same in the both contrast conditions (see Figure 3). Although the difference was not found to be statistically significant in the overall analysis, four out of five chimpanzees found it easier to match half-faces in the misaligned condition compared to the aligned equivalent when the contrast of the stimuli had been reversed (see Table 1). The loss of statistical power could be

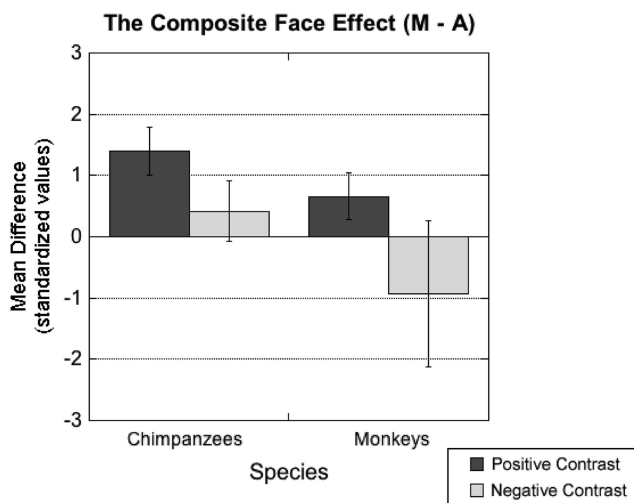


Figure 3. Mean difference between performance in the misaligned and aligned trials (error bars represent 95% Confidence Intervals) for chimpanzees and monkeys in each of the contrast conditions (positive contrast and negative contrast).

attributed to the smaller effect size associated with the CFE for negative faces. Indeed, experiments that have tested larger samples of adult humans have sometimes failed to find a significant advantage for misaligned trials (e.g., Hole et al., 1999). Thus, this study provides a reason to believe that chimpanzees respond to faces in a similar way to humans but more research is needed to determine whether chimpanzees build holistic representations of negative contrast faces.

On the other hand, the performance of the rhesus monkeys in the negative contrast condition was counter to prediction (see Figure 3). In general, the rhesus monkeys found matching half-faces more difficult than the chimpanzees, with only three out of six subjects passing the performance criterion and, more to the point, the differences between aligned and misaligned performance indicate that the CFE was strictly limited to the positive contrast condition. Above chance accuracy in the control condition provides some indication that the three rhesus monkeys included in the analysis were able (and motivated) to do the task with negative contrast stimuli and yet not one subject was more accurate in the misaligned trials than in the aligned trials (see Table 1). A strength of this study was that no preexperimental training took place over-and-above the subject's extensive practice with the MTS procedure. This approach helps to rule out a simple bias against misaligned trials as an explanation for the negative contrast result. Furthermore, using the same testing procedure, we were able to find evidence of a CFE in the positive contrast condition, suggesting that the method was sensitive to holistic processing. Therefore, based on these current data, we propose that holistic processing may operate differently in rhesus monkeys than in humans. We will now consider the theoretical implications of this proposal.

Human adults find contrast-reversed faces hard to recognize (Bruce & Langton, 1994; Galper, 1970). Nonetheless there is evidence that holistic processing operates on positive and negative faces (Hole et al., 1999). Maurer, Le Grand, and Mondloch (2002) use this dissociation to support their view that holistic processing occurs before individual faces are recognized, as information derived from typical shading in positive contrast images is necessary for individual recognition (Kemp, Pike, White, & Musselmen, 1996). Tsao and Livingstone (2008) go one step further to suggest a link between face detection and holistic processing which might account for the preserved CFE, found in seven out of eight patients with a selective impairment of individual face recognition or prosopagnosia (Le Grand, et al., 2006). There is evidence, therefore, that holistic processing is independent of individual face recognition (Konar et al., 2010) and these data suggest that holistic processing might be tuned differently in rhesus monkeys than in humans (Hole et al., 1999). This result raises a set of interesting questions about the evolution and ontogeny of holistic processing in primate species. These questions might be easier to answer if there was a straightforward explanation for the effect of contrast-reversal on human face recognition. Bruce and Langton (1994) argued that familiar faces are harder to recognize when they are presented as photographic negatives because contrast reversal changes skin texture and pigmentation. Perhaps, then, rhesus monkeys are more sensitive to contrast-polarity in this experiment because color transmits the signal for holistic processing whereas color on a human (or chimpanzee) face serves as a second-order property that supports individual recognition but is not necessary for holistic processing in the first instance. In the study of contrast

reversal published by Parr and Taubert (2011), these same subjects were trained with a set of positive (grayscale) faces then tested with the same set of faces after the RGB color profile had been restored (color) or contrast was reversed (negative). While performance for both species was impaired by contrast-reversal, the chimpanzees tolerated the introduction of color whereas the rhesus monkey performance in the color condition did not completely recover. This provides further support for the idea that surface information is more important for matching individual identity in rhesus monkeys.

The results of this study form part of a larger pattern that is emerging in comparative research where rhesus monkey behavior deviates from predictions based on human or chimpanzee behavior. In a recent comparative study, the present subjects were tested for their sensitivity to geometric stretching in a face-matching task (Taubert & Parr, 2011). A manipulation of familiarity revealed that there was a pronounced difference in the way chimpanzees analyzed unfamiliar and familiar conspecific faces. This difference was reminiscent of results reported in studies of human behavior (Bruce et al., 1999; Bruce, Henderson, Newman, & Burton, 2001; Bruce & Young, 1986; Burton, Jenkins, Hancock, & White, 2005). In contrast, the experiment indicated that rhesus monkeys approached all faces uniformly, regardless of familiarity (Taubert & Parr, 2011). An earlier study that used the FIE as a marker of face-like expertise have found that, counter to prediction, that inversion disrupted the individual discrimination of conspecific's faces and capuchin faces (Parr, Winslow, & Hopkins, 1999) which was confirmed by a later study which observed the FIE in three categories of faces, (conspecifics, humans, and chimpanzees; Parr et al., 2008). These studies, and others like them (Gothard, Erickson, & Amaral, 2004; Parr & Henitz, 2008), converge to suggest that visual expertise does not predict the FIE in rhesus monkeys. Meanwhile, previous studies of both humans and chimpanzees have found that the FIE only occurs for faces subsequent to the acquisition of expertise (*humans*, Diamond & Carey, 1986; Tanaka & Farah, 1991; Yin, 1969; *chimpanzees*, Parr, Dove, Hopkins, 1998; Parr & Heintz, 2006; Tomonaga, 2007). It has been argued elsewhere that the basis for these interesting species differences might be social complexity driving cognitive specializations in humans and chimpanzees (Amici, Aureli, & Call, 2008; Parr, 2011; Parr et al., 2008; Taubert & Parr, 2009). These differences in behavioral responses, although slight, warrant further investigation as they have broad implications for evolutionary psychology and comparative neurology.

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Correction to DeCarlo, and Abramson (1989)

In the article “Time Allocation in Carpenter Ants (*Camponotus herculeanus*),” by Lawrence T. DeCarlo, and Charles I. Abramson (*Journal of Comparative Psychology*, Vol. 103, No. 4, pp. 389–400), there was an error in the spelling of the species of ant discussed. “Componotus herculeanus” should read “Camponotus herculeanus”. All versions of this article have been corrected.

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