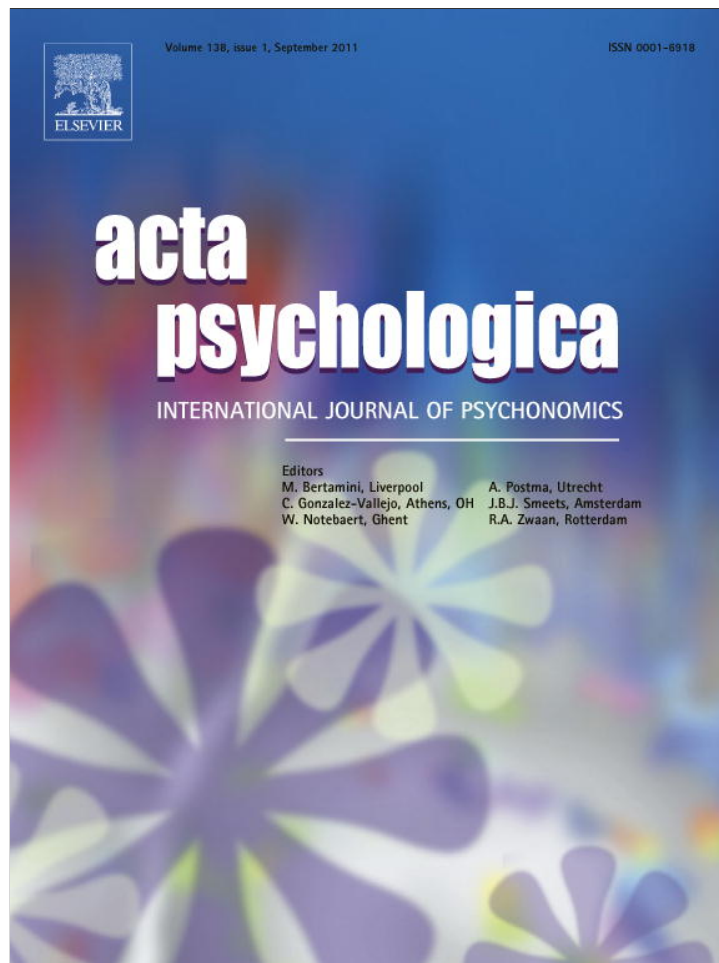


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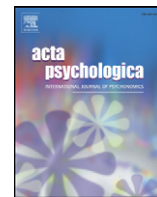
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The inversion effect reveals species differences in face processing

Lisa A. Parr*

Division of Psychiatry and Behavioral Sciences & Center for Translational Social Neuroscience, Emory University, Atlanta, GA 30322, USA
Yerkes National Primate Research Center, Emory University, Atlanta, GA 30329, USA

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ABSTRACT

Face recognition is a complex skill that requires the integration of facial features across the whole face, e.g., holistic processing. It is unclear whether, and to what extent, other species process faces in a manner that is similar to humans. Previous studies on the inversion effect, a marker of holistic processing, in nonhuman primates have revealed mixed results in part because many studies have failed to include alternative image categories necessary to understand whether the effects are truly face-specific. The present study re-examined the inversion effect in rhesus monkeys and chimpanzees using comparable testing methods and a variety of high quality stimuli including faces and nonfaces. The data support an inversion effect in chimpanzees only for conspecifics' faces (expert category), suggesting face-specific holistic processing similar to humans. Rhesus monkeys showed inversion effects for conspecifics, but also for heterospecifics' faces (chimpanzees), and nonfaces images (houses), supporting important species differences in this simple test of holistic face processing.

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1. Introduction

The inversion effect refers to a relative impairment in the ability to discriminate faces when they are turned upside down compared to when they are in their typical upright orientation (Valentine, 1988; Yin, 1969). Among humans, the inversion effect is augmented by stimulus categories for which people have developed expertise, like human faces. Because there is no other natural stimulus category for which we garner as much expertise from birth as faces, it has often been assumed that the inversion effect is face-specific. Several studies, however, have shown impairments in the discrimination of other highly familiar stimulus categories for which there are many individual exemplars, such as dogs, sheep, and birds, including trained categories of man-made objects, like Greebles (Diamond & Carey, 1986; Gauthier & Tarr, 1997). Although the effect of inversion is not as detrimental to the recognition of Greebles as it is for faces (Gauthier et al. 1999; McKone & Yovel, 2009; Robbins and McKone 2007), the data, nonetheless, confirm the important role of expertise in holistic processing and help to explain why the effect of inversion on faces is so robust. Throughout this paper, we use the term expertise to refer to developmental familiarity with conspecifics' faces, and the special (expert) status that these faces have in eliciting cognitive specializations in humans.

There is some disagreement on the underlying cause of the inversion effect. Some authors suggest that the inversion effect is due to impairments in the ability to extract 2nd order configural information from an inverted face. Second-order configural cues refer to the relative size and spacing of features (Diamond & Carey, 1986; Freire, Lee, & Symons, 2000; Maurer, Le Grand, & Mondloch, 2002). These claims are supported by studies that show quantitatively greater inversion effects when subjects are required to utilize the spacing of features compared to the identity of features when discriminating faces (Mondloch, Geldart, Maurer, & Le Grand, 2003). An alternative account, however, suggests that the inversion effect results as a consequence of holistic processing for upright faces and thus can be used as a marker of holistic face processing (Rossion, 2008). This holistic approach refers to a perceptual process whereby the features of a face, their relative size, placement, and spacing, are simultaneously integrated into a perceptual whole (Tanaka & Farah, 1993). The inability to extract holistic information from an inverted face qualitatively shifts the strategy towards detecting spacing differences. Moreover, in several classic tasks of holistic processing, the effects are minimized or eliminated when the stimuli are inverted. The composite face effect, for example, is a task that combines the upper and lower face parts of two different individuals. The effect is that the individual in the upper face part is easier to identify when it is offset from the lower part, disengaging holistic processing, compared to when the face parts are aligned in a face-like configuration (Young, Hellawell, & Hay, 1987). The misaligned advantage disappears when the faces are inverted because inverted faces do not engage holistic processing. Similarly, the Thatcher illusion, the grotesque appearance

* Yerkes National Primate Research Center, 954 Gatewood Rd., Atlanta, GA 30329 USA. Tel.: +1 404 727 3653; fax: +1 404 727 8088.
E-mail address: lparr@emory.edu.

of faces after selective inversion of the eyes and the mouth in an upright face, disappears when the faces are inverted (Thompson, 1980). Finally, the other-race effect, poorer discrimination of faces from an unfamiliar race, is believed to result from the lack of holistic processing for other-race faces. Deficits in identifying own versus other-race faces disappears when the faces are inverted (Rhodes, Brake, Taylor, & Tan, 1989; Sangrigoli & de Schonen, 2004). While it is not the purpose of this paper to disentangle whether the inversion effect is a cause or consequence of holistic processing, these studies confirm the important relationship between these two face processing phenomena.

There is also considerable debate about whether the numerous face processing specializations observed in humans are shared by other species or whether they reflect true cognitive specializations. As is the case for the human literature, the inversion effect is by far the most widely tested phenomenon in comparative face recognition studies, but the results of these studies have been inconsistent and difficult to interpret for several reasons. The main source of this confusion is whether conspecifics' faces share a special status in holistic processing, eliciting stronger inversion effects than heterospecific faces or nonface stimuli, in nonhuman primates that is comparable to human reports (Parr, 2011 for a detailed review of this literature). In brief, studies of inversion effects in chimpanzees report consistent findings. Using a matching-to-sample (MTS) task, Parr, Dove and Hopkins (1998) found clear expertise effects in five chimpanzees. Subjects were significantly worse discriminating inverted compared to upright faces of expert categories only (chimpanzee and human faces), but no significant inversion effects were found for unfamiliar, heterospecific faces (capuchin monkeys) or nonface categories (automobiles or clip art). Using a similar MTS task format, Tomonaga (1999) found the inversion effect for unfamiliar human faces compared to houses in one chimpanzee. The same subject was significantly faster identifying upright human faces compared to upright chairs or hands in a visual search task (Tomonaga, 2007). A follow-up study showed that chimpanzees were faster to identify the inner features of an upright face compared to inverted distracters (Tomonaga, 2007).

In contrast to chimpanzees, data on inversion effects in monkeys are inconsistent and often fail to support a special status for conspecifics' faces, or even face-selective effects more generally. Some studies have reported evidence of the face inversion effect in monkeys (Neiworth et al. 2007-cotton-top tamarins; Overman and Doty 1982-pigtail macaques; Tomonaga 1994-Japanese macaques; Vermeire and Hamilton 1998-rhesus monkeys), while others have failed to find evidence of inversion effects specific for faces (Bruce 1982; Dittrich 1990-longtail macaques; Gothard et al. 2004; Parr, Winslow, & Hopkins, 1999; Rosenfeld and van Hoesen 1979-rhesus monkeys; Weiss et al. 2001-cotton-top tamarins). When rhesus monkeys were tested using procedures comparable to chimpanzees, Parr and colleagues (1999) reported inversion effects for conspecifics' faces, unfamiliar capuchin monkey faces, and automobiles, but not human faces (which could have been considered an expert category as the monkeys were born and raised in captivity with human caregivers), or clip art (Parr et al., 1999). Using an identical testing method in a separate group of rhesus monkeys, inversion effects were found for conspecifics' faces, human faces, and unfamiliar chimpanzee faces, but not houses or clip art (Parr, Heintz, & Pradhan, 2008). Using eye-tracking as a dependent measure in rhesus monkeys, Gothard et al. (2009) demonstrated a reduction eye-fixations when subjects viewed inverted compared to upright conspecifics, but not human faces. These authors speculated that monkeys have different perceptual strategies for processing conspecifics' faces compared to human faces. Using a similar methodology in rhesus monkeys, Dahl et al. (2009) also reported reduced fixations to the eye region of inverted conspecifics compared to human faces. In both of these studies, no control stimuli were used to assess the face-selectivity of the scan patterns, and the monkey subjects were all born and raised in

captivity by humans, so the quality of the expertise manipulation was also unclear.

Because of continued debate in the literature concerning similarities and differences in the face processing strategies of humans and nonhuman primates, we present data from a new series of inversion studies in both chimpanzees and rhesus monkeys. The testing methods were directly comparable and the stimuli contained both conspecific (expert) and heterospecific (nonexpert) faces, as well as several complex nonface categories (shoes, houses and clip art). The goal was to directly compare the face-selectivity of inversion effects in two species of nonhuman primates using comparable methods. Consistent with previous studies, we hypothesized that both chimpanzees and rhesus monkeys would show inversion effects for conspecifics' faces (Dahl, Wallraven, Bülhoff, & Logothetis, 2009; Gothard, Brooks, & Peterson, 2009; Parr, Dove, & Hopkins, 1998; Parr et al., 1999; Parr et al., 2008). In contrast to the monkeys, however, we predicted that the inversion effects for chimpanzees would be shown exclusively for conspecifics' faces. We also predicted that the inversion effects shown by rhesus monkeys would extend to other categories, in addition to conspecifics' faces, including both face and nonface categories. We report all training data in an effort to alleviate concerns about unusual responses biases in operant procedures (Adachi, Chou, & Hampton, 2009; Dahl, Logothetis, & Hoffman, 2007). Finally, researchers have recently cautioned that any reports of face-specific inversion effects should account for general impairments that occur when stimuli are inverted (Crookes & McKone, 2009). To address this, we present an additional analysis using inversion scores for each stimulus category that have been adjusted by the general costs shown by each subject for inverted clip art.

2. General methods

2.1. Subjects

Six chimpanzees (4 males, 2 females) participated in these studies ranging in age from 16 to 22 years. These subjects were all raised by humans in peer groups in the Yerkes Primate Center nursery until 4 years of age when they joined established social groups consisting of a range of older individuals. All subjects had extensive experience performing computerized tasks of face recognition using MTS prior to the onset of these studies (Parr & Hecht, 2011). All subjects were socially housed and tested voluntarily in their home cage using a computerized-joystick testing system.

Six rhesus monkeys (2 males, 4 females born in 2000 and 2001) participated in these studies. Four subjects were 8 years of age when tested and 2 females were 7 years of age. They were each born into large social groups at the Yerkes National Primate Research Center's field station, Lawrenceville, GA and in 2004, they moved to the main campus to participate in experimental studies of social cognition. At this time, they were housed in same-sex pairs in the same home room, and tested daily in their home cage using a custom designed touchscreen computer system (see Parr et al., 2008). This consisted of a 15" acoustic wave touchscreen (Elo touch) that could be inserted into the doorway of the home cage for access without obstruction from caging. Treats were delivered to a small cup located beneath the touchscreen. All subjects had extensive experience performing computerized tasks of face recognition using matching-to-sample (MTS) prior to this study (see Parr et al., 2008; Parr & Heintz, 2006). All testing was voluntary.

2.2. Stimuli

All stimuli consisted of high-quality digitized images presented on the computer using a stimulus height of 300 pixels and 150 dpi. Chimpanzee and rhesus monkey face images were acquired from colonies living at the Yerkes National Primate Research Center field

station or other facilities in the United States and they depicted individuals who were personally unfamiliar to the subjects. Images of houses and clip art were downloaded from the World Wide Web. Shoes were collected from employees working at the Yerkes Primate Center and photographed under standardized lighting conditions against a black background. These images are available upon request from the author. All images were presented in 256 grayscale and edited so as to exclude background information. Fig. 1 shows several examples from each stimulus category.

2.3. Procedures

All subjects were tested using computerized matching-to-sample (MTS) tasks in the home cage. Chimpanzees performed these tasks using a joystick-controlled cursor while monkeys performed the same tasks using a touchscreen interface. According to the MTS procedure, subjects are first shown a single image on the computer monitor, referred to as the sample, or the image to match. This was presented centrally against one of the four sides of the computer monitor. After orienting to this image, either by contacting it with the joystick-controlled cursor (chimpanzee), or touching it three times in rapid succession on the touchscreen (rhesus monkey), two additional images appeared simultaneously on the screen located equidistant from the sample on the opposite side of the monitor. One of these images (target) was identical to the sample while the other (foil) was a different exemplar from the same category, e.g., another conspecific's face, another shoe, etc. A correct response to the target was followed by a food reward and an inter-trial interval (ITI) of 2 s, while an incorrect response to the foil was followed by an ITI of 6 s and no food reinforcement. The next trial was then presented.

There were 15 unique trials included for each stimulus category. Clip art trials were presented first, followed by the house task. Then half the subjects received conspecific's faces while the other half received shoes. These were then swapped so the first group received shoes and the second group received conspecific's faces. Hetero-specific's faces were presented last in an effort to add a nonexpert face

category. This consisted of showing the rhesus monkey faces to the chimpanzees and the chimpanzee faces to the rhesus monkeys. These were the exact same images as shown in the conspecific trials. These 15 trials were repeated four times in a daily testing session, totaling 60 trials per session. For the purpose of this experiment, subjects were tested on upright trials until their performance exceeded 85%. After reaching this criterion, the two comparison choices (target + foil) were inverted (rotated 180°) and these 15 inverted trials were added to the original 15 training trials, totaling 30 trials. In all trials, the sample always remained upright. Fig. 2 illustrates an upright and inverted MTS trial showing a chimpanzee face. Subjects were given only 4 repetitions of these 30 test trials in 2 separate testing sessions for a total of 120 trials, 60 were original upright and 60 were inverted.

2.4. Data analysis

First, the number of sessions required to reach the task criterion on upright stimuli was compared to evaluate species differences in learning each stimulus category. This was done using an independent sample *t*-test where species was the between-subject factor. The inversion task data were then analyzed by comparing subjects' performance (% correct responses) on upright compared to inverted trials using repeated measures ANOVAs where species was the between-subjects factor and orientation (upright vs. inverted) was the within-subjects factor.

Additionally, it has been recently recommended that any evaluation of inversion costs for faces or other stimuli needs to be controlled for by the general impairments that result when stimuli are presented in atypical orientations (Crookes & McKone, 2009). Thus, a separate analysis was performed on the difference scores (%upright – %inverted = Difference Index) for each stimulus category after adjusting these scores for the overall inversion costs on the clip art stimuli (used as a general control category). To do this, a DI was calculated for each stimulus category. Then, the DI scores for clip art were subtracted from the DI scores for every other category (adjDI). For example, if a subject showed a moderate inversion effect for houses, e.g., DI of 8%, but also a small inversion effect for clip art,

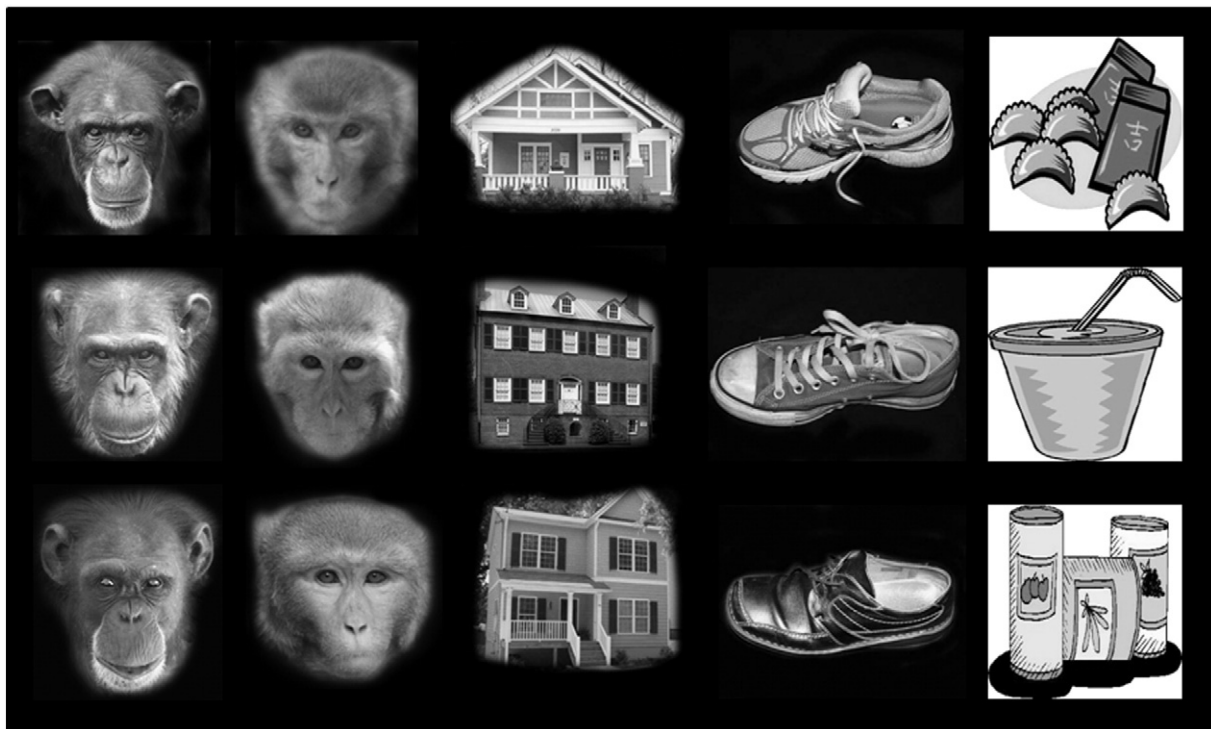


Fig. 1. Three examples of the five stimulus categories, from left to right chimpanzee face, rhesus face, house, shoe and clip art. These images are available upon request from the author.

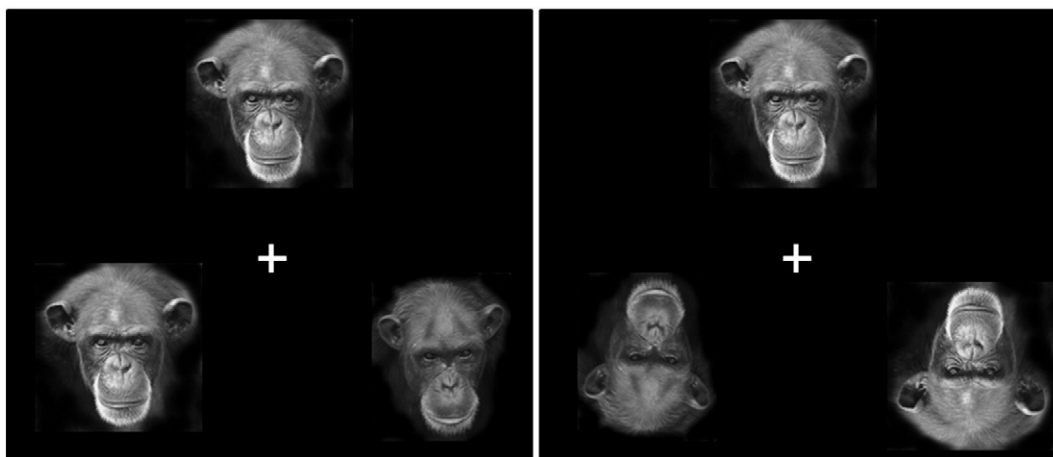


Fig. 2. An illustration of an upright and inverted MTS trial showing chimpanzee faces.

e.g., DI of 4%, their adjDI for houses would be reduced to 4%. If a subject failed to show an inversion effect for houses, e.g., DI of -8% , but did show an inversion effect for clip art, the lack of inversion for houses would be amplified in their adjDI score, -12% . In contrast, if a subject showed an inversion effect for houses, e.g., DI of 8% , but failed to show an inversion effect for clip art, e.g., DI score, -4% , their inversion effect for houses would be amplified in an adjDI value of 12% . After calculating the adjDI scores for each stimulus category, independent t-tests were used to compare species differences. All p-values are set at $p < 0.05$ (two-tailed).

3. Results

Fig. 3 shows the performance on upright and inverted trials for all stimulus categories for both chimpanzees and rhesus monkeys.

3.1. Clip art

Repeated measures ANOVAs revealed no significant effect of orientation for clip art, $F(1,10) = 0.48$, $p = 0.50$ and no interaction between species and orientation, $F(1,10) = 0.03$, $p = 0.87$. The main effect of species was borderline but not significant, $F(1,10) = 4.38$, $p = 0.063$. There was no significant species difference between the number of sessions required to exceed the initial performance criterion on upright stimuli: chimpanzee (mean = 2.83, SEM = 1.08), rhesus monkeys (mean = 6.33, SEM = 2.47), $t(10) = 1.30$, $p = 0.22$. During the

inversion test sessions, the chimpanzees (mean = 91.67%, SEM = 1.02) showed a higher overall performance on the upright stimuli than rhesus monkeys (mean = 84.83%, SEM = 2.87), $t(10) = 2.24$, $p = 0.049$.

3.2. Houses

Two subjects (one chimpanzee and one rhesus monkey) failed to reach the training performance criterion ($>85\%$ correct) on the upright houses after completing 20 sessions, 1200 total trials or 80 repetitions of each of the 15 novel house trials. These subjects did not perform the inverted sessions and were removed from the subsequent analyses. The following analyses of inversion effects for houses were conducted with 5 chimpanzee and 5 rhesus monkey subjects. Repeated measures ANOVAs revealed a significant effect of orientation for houses, $F(1,8) = 6.04$, $p = 0.039$, and a significant interaction between species and orientation, $F(1,8) = 13.45$, $p = 0.006$. The main effect of species was not significant, $F(1,8) = 1.09$, $p = 0.33$. To follow-up the significant interaction of orientation by species, paired t-tests compared each species performance on upright compared to inverted houses. This revealed a significant inversion effect for the rhesus monkeys, $t(4) = 3.26$, $p = 0.03$, but no significant difference in performance on upright compared to inverted trials for the chimpanzees, $t(4) = 1.77$, $p = 0.15$ (see Fig. 3). There was no significant species difference in the number of sessions required to exceed the initial performance criterion on upright stimuli: chimpanzee (mean = 6.60, SEM = 1.33), rhesus monkeys (mean = 11.00, SEM = 1.84), $t(8) = 1.94$, $p = 0.09$. During the inversion test sessions, the chimpanzees (mean = 76.80%, SEM = 2.15) showed a lower overall performance on the upright stimuli than rhesus monkeys (mean = 85.66%, SEM = 2.52), $t(8) = 2.68$, $p = 0.03$.

3.3. Shoes

Repeated measures ANOVAs revealed no significant effect of orientation for shoes, $F(1,10) = 0.57$, $p = 0.47$ and a near but not significant interaction between species and orientation, $F(1,10) = 4.63$, $p = 0.06$. The main effect of species was not significant, $F(1,10) = 0.46$, $p = 0.51$. There was no significant species difference in the number of sessions required to exceed the initial performance criterion on upright stimuli: chimpanzee (mean = 9.50, SEM = 3.68), rhesus monkeys (mean = 11.50, SEM = 2.36), $t(10) = 0.46$, $p = 0.66$. There was also no significant difference between the performance of monkeys and chimpanzees on the upright trials during the inversion test sessions; chimpanzees (mean = 76.11%, SEM = 2.81) and rhesus monkeys (mean = 79.72%, SEM = 3.61), $t(10) = 0.79$, $p = 0.45$.

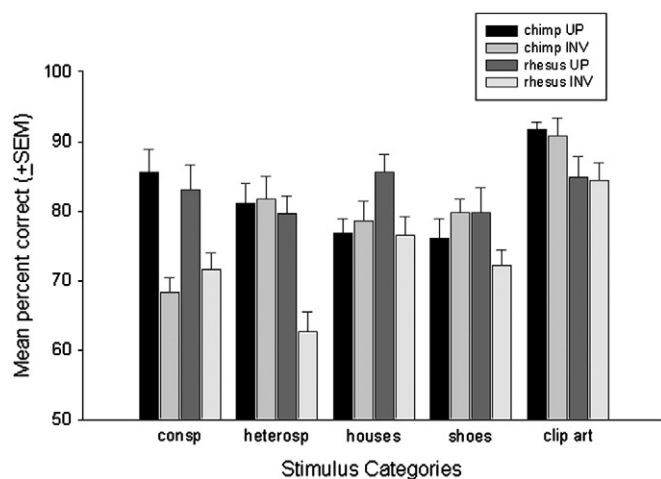


Fig. 3. Mean performance on upright and inverted images from five stimulus categories.

3.4. Heterospecific faces

Two rhesus monkeys failed to reach the upright training criteria for heterospecific faces after 20 sessions, or 1200 total trials. This represents 80 repetitions of the 15 unique trials in this task. One subject exceeded 70% only twice in 20 sessions and her data were excluded from subsequent analyses. The second subject's performance on the final 3 training sessions (18th, 19th and 20th) was 80%, 80% and 75.56%. It was determined that her performance was good enough to be included in the overall data analysis, but she was excluded from the analysis of number of sessions to criterion because she never actually reached the a priori level.

Repeated measures ANOVAs revealed a significant main effect of orientation for heterospecific faces, $F(1,9) = 15.11$, $p = 0.004$, a significant interaction between species and orientation, $F(1,9) = 17.22$, $p = 0.002$, and a significant main effect of species, $F(1,9) = 8.09$, $p = 0.02$. To follow-up the significant interaction of orientation by species, paired t-tests compared each species performance on upright compared to inverted heterospecific faces. This revealed a significant inversion effect for the rhesus monkeys when required to discriminate chimpanzee faces, $t(4) = 4.17$, $p = 0.015$, but no significant difference in performance on upright compared to inverted trials for the chimpanzees when required to discriminate rhesus monkey faces, $t(5) = 0.31$, $p = 0.77$ (see Fig. 3). There was no significant species difference in the number of sessions required to exceed the initial performance criterion on upright stimuli: chimpanzee (mean = 5.5, SEM = 1.78), rhesus monkeys (mean = 7.75, SEM = 2.93), $t(8) = 0.70$, $p = 0.50$, nor was there any significant species difference in performance on upright trials during the inversion test sessions, chimpanzees (mean = 81.11%, SEM = 2.81) and rhesus monkeys (mean = 79.67%, SEM = 2.44), $t(9) = 0.38$, $p = 0.71$.

3.5. Conspecific faces

Repeated measures ANOVAs revealed a significant main effect of orientation for conspecifics' faces, $F(1,10) = 24.81$, $p = 0.001$. There was no significant difference for species, $F(1,10) = 0.02$, $p = 0.89$, or significant interaction between species and orientation, $F(1,10) = 1.03$, $p = 0.33$. To follow-up the main effect, paired t-tests compared the performance on upright compared to inverted trials for each species. This revealed significant inversion effects for both chimpanzees, $t(5) = 4.51$, $p = 0.006$, and rhesus monkeys, $t(5) = 2.65$, $p = 0.045$ (see Fig. 3). There was no significant differences between the number of sessions required to exceed the initial performance criterion on upright stimuli: chimpanzee (mean = 5.67, SEM = 2.06), rhesus monkeys (mean = 9.83, SEM = 2.27), $t(10) = 1.36$, $p = 0.20$, nor was there any significant species difference in performance on upright trials during the inversion test sessions, chimpanzees (mean = 85.56%, SEM = 3.35) and rhesus monkeys (mean = 83.05%, SEM = 3.53), $t(10) = 0.51$, $p = 0.62$.

3.6. Difference-index adjusted for general inversion costs

Fig. 4 illustrates the mean adjusted DI scores (adjDI) for each stimulus category, indicating the magnitude of the inversion effect for each species when adjusted for overall inversion costs for clip art. Independent t-tests revealed significant species differences for adjDI scores for heterospecific faces, $t(10) = 3.02$, $p = 0.013$; houses, $t(8) = 3.67$, $p = 0.006$; and a borderline species difference for shoes, $t(10) = 1.97$, $p = 0.08$. No species difference in adjDI scores was observed for conspecifics faces, $t(10) = 1.09$, $p = 0.30$.

4. Discussion

Using identical stimuli and comparable testing methods, these data show clear species differences in holistic processing, assessed

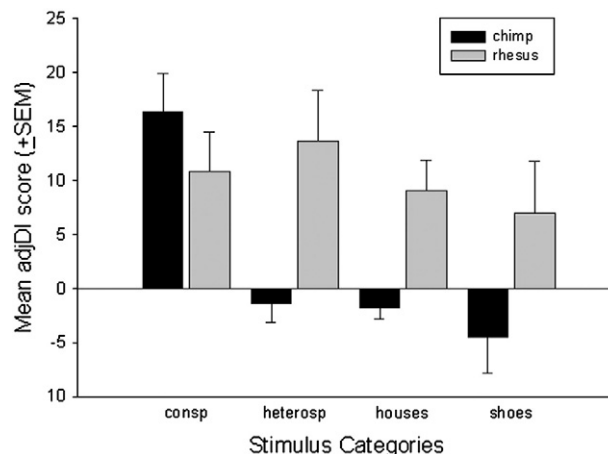


Fig. 4. Mean adjusted DI score showing the magnitude of the inversion effect for each stimulus category.

using the face inversion effect. Chimpanzees showed the inversion effect for conspecifics' faces only, not heterospecifics' faces (rhesus monkeys), houses, shoes, or clip art images. Therefore, for chimpanzees, the inversion effect appears to operate only on the most expert stimulus category, e.g., conspecifics' faces, not unfamiliar faces or nonface categories. This replicates previous findings in this species and, like humans, confirms the special status that conspecific faces have in eliciting holistic processing (Parr et al., 1998; Parr & Heintz, 2006; Parr, 2011; Tomonaga, 2007). It is presumed that the special status of conspecifics' faces comes from the extensive experience gained with this stimulus category throughout development and in daily interactions with other chimpanzees. Despite similar familiarity with conspecifics' faces, rhesus monkeys showed significant inversion effects for all faces, conspecific and heterospecific (chimpanzee faces), as well as for houses. In addition, the cost for discriminating inverted shoes neared significance. No inversion effect was seen in either species for discriminations involving clip art images. These results support previous findings from our lab suggesting that the inversion effect in rhesus monkeys is not face-selective, occurring only for a special category of faces, e.g., conspecifics' faces, nor is it face-specific, occurring only for faces compared to nonface images (Parr, 2011; Parr et al., 1999; Parr & Heintz, 2008).

As a separate analysis of the inversion effect, we adjusted the difference scores between performance on upright and inverted trials based on the overall cost of inversion shown for the clip art trials. Changing the orientation of stimuli between the training and test trials is expected to produce a deficit in performance regardless of the identity of the stimulus categories. Our choice to adjust performance using the results from the clip art trials was based on previous data from numerous studies in our lab showing that clip art fail to reveal significant inversion costs. Therefore, general impairments on inverted clip art were used to compensate for the general costs of changing the quality (orientation) of stimuli between the training and test trials, and not differences in cognitive and/or perceptual processing strategies. However, it could also be argued that clip art does not reflect a stimulus category for which there are many within-category exemplars, like faces, and therefore may not be the most appropriate category. If, however, one were to utilize a different category, such as houses, the magnitude of inversion effects shown by the monkeys would be reduced, as houses revealed significant inversion effects. For example, for conspecific faces, the DI score adjusted for clip art was 10.78%, but when this was adjusted for houses, it dropped to 0.22%. The chimpanzees, however, showed slightly better performance discriminating inverted compared to upright houses, so the magnitude of their inversion effects would be increased if houses were chosen. For conspecific faces, the DI score

adjusted for clip art was 16.39%, but when adjusted for houses this increased to 22.13%. These adjustments for the inversion effect in rhesus monkeys highlights the important finding; that the conspecific face lacks special status for the rhesus monkeys compared to the chimpanzee. Regardless of the approach taken, the results of these studies reveal significant species differences in the pattern of inversion effects and confirm the importance of holistic processing for conspecifics' face in the chimpanzee, similar to humans.

Previous studies in monkeys have utilized the inversion effect as a marker for holistic processing and concluded that rhesus monkeys show face-selective holistic processing, just like humans (Adachi et al., 2009; Dahl et al., 2009). This requires that the inversion costs for conspecifics' faces be compared to the results from both nonexpert face and nonface categories, but neither control was used in these studies. Without such comparisons, no conclusions can be made about the importance of holistic processing for conspecifics' faces or its similarity to humans. Adachi et al. (2009) reported similar face processing strategies between humans and monkeys using the Thatcher Illusion (Bartlett & Searcy, 1993; Thompson, 1980). This is a test of holistic processing as it shows that information about the specific features of a face, e.g., orientation of the eyes and mouth, is hard to extract when the features are embedded in the context of a whole face (Tanaka & Farah, 1993). Moreover, this effect is minimized when the faces are inverted, implicating its dependence on holistic processing. Using a viewing preference paradigm, monkeys looked longer at upright compared to inverted thatcherized faces, suggesting that they share similar face processing mechanisms as humans (Adachi et al., 2009). This conclusion is premature, however, because the study failed to utilize any control stimuli, e.g., thatcherized faces of another species, or other manipulated nonface categories, to confirm that the effect was indeed selective for conspecifics' faces. Problematically, what is often concluded from these and similar studies is that if monkeys show the inversion effect then, like humans, they must be sensitive to 2nd order configural cues. This is an important comparative issue as the ability to utilize 2nd order configural cues in humans requires a protracted period of development (Mondloch et al., 2003) and is used to define adult-levels of expertise (Crookes & McKone, 2009). Moreover, whether monkeys are sensitive to the spacing of facial features has only been directly tested a few times with different results (Dahl et al., 2007; Parr et al., 2008; Sugita, 2008). Therefore, considerably more testing is needed before any conclusions can be drawn about species similarities or differences in sensitivity to both holistic processing and 2nd order cues in faces.

There are some discrepancies in our published data from chimpanzees that should be discussed. Parr et al. (1998) reported evidence of the inversion effect in chimpanzees for human faces, presumed to be an expert category, as subjects were raised in peer-groups by humans in the primate center nursery. However, a decade later, Parr et al. (2008) failed to demonstrate holistic processing for human faces in the same chimpanzee subjects using the composite face task, another task of holistic processing (Young et al., 1987). Although the exact cause of this discrepancy may never be known, it is very likely that a change in the chimpanzees' expertise with human faces is responsible. Chimpanzees in both studies (4 of the same subjects were included in both studies) were all reared by humans in the Yerkes Primate Center nursery during the late 1980's. After moving into the main colony at 4 years of age, the chimpanzees' experience with humans was almost exclusively limited to caretakers and researchers wearing personal protective equipment (PPE), e.g., masks, face shields, hair covers, a procedure that was uncommon in the nursery. In the event that humans were seen without PPE, it was by regulation at a considerable distance from the subject and viewing distance is a critical factor in the ability to integrate facial features via holistic processing (McKone, 2009). Therefore, the earlier expertise shown by chimpanzees for human faces appears to have diminished as their visual experience with human faces (not wearing PPE) became more restricted. It is because of this uncertain degree of

expertise with human faces that they were not used in the present study.

There is no doubt that face processing is a complex and highly specialized skill in humans and the extent to which nonhuman primates share these skills, and to what degree, is a fascinating question in comparative social cognition. Researchers should be careful to design well-controlled experiments and be cautious in their interpretations so that this literature can move forward progressively. Moreover, discrepancies in the literature should not be ignored (Dahl et al., 2009), or pushed aside as mere testing biases (Adachi et al., 2009; Dahl et al., 2009), as these discrepancies are a source of valuable information and addressing them directly is the only way to advance our understanding of the evolution of face processing skills in primates.

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