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ORIGINAL PAPER

How the Thatcher illusion reveals evolutionary differences in the face processing of primates

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Abstract Face recognition in humans is a complex cognitive skill that requires sensitivity to unique configurations of eyes, mouth, and other facial features. The Thatcher illusion has been used to demonstrate the importance of orientation when processing configural information within faces. Transforming an upright face so that the eyes and mouth are inverted renders the face grotesque; however, when this "Thatcherized" face is inverted, the effect disappears. Due to the use of primate models in social cognition research, it is important to determine the extent to which specialized cognitive functions like face processing occur across species. To date, the Thatcher illusion has been explored in only a few species with mixed results. Here, we used computerized tasks to examine whether nonhuman primates perceive the Thatcher illusion. Chimpanzees and rhesus monkeys were required to discriminate between Thatcherized and unaltered faces presented upright and inverted. Our results confirm that chimpanzees perceived the Thatcher illusion, but rhesus monkeys did not, suggesting species differences in the importance of configural information in face processing. Three further experiments were conducted to understand why our results differed from previously published accounts of the Thatcher illusion in rhesus monkeys.

Keywords Visual illusion · Face recognition · Chimpanzee · Rhesus monkey · Evolution · Matching-to-sample

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Introduction

Humans are remarkably skilled at detecting subtle differences between thousands of individual faces. This is facilitated through the holistic integration of facial features into a single perceptual whole and is dependent on the face being viewed in its canonical orientation. When faces are presented upside down, our ability to detect the unique configuration of facial features becomes disrupted, and as a result, face discrimination becomes more difficult (Rhodes et al. 1989; Rossion 2008; Valentine 1988; Yin 1969) Further evidence for the importance of orientation in face processing emerges through an effect first described by Thompson (1980) as the "Thatcher illusion," originally demonstrated using an image of Margaret Thatcher's face. When the eyes and mouth of a face are rotated 180 degrees in an upright face, the image appears "grotesque" compared to the unaltered original. However, when the whole image is inverted 180 degrees, the configural changes are undetected, and the striking abnormality is reduced. While the exact mechanism underlying the Thatcher illusion remains unknown, it provides a vivid example of how essential canonical orientation is for the processing of interconnectivity between facial features and, ultimately, discriminating between individuals.

In order to understand whether the Thatcher illusion demonstrates a unique cognitive specialization for face

processing in humans, it is important to examine this phenomenon in related species and compare the findings. While the Thatcher illusion has been examined extensively in humans (Bartlett and Searcy 1993; Donnelly and Hadwin 2003; Leder et al. 2001), it has been explored sparingly in nonhuman primates, with mixed results. Parron and Fagot (2008) used a two-choice forced-discrimination task to reveal that baboons (*Papio papio*) could learn to discriminate between two different baboon faces or two human faces, but did not learn whether these faces had been Thatcherized. These authors concluded that the cognitive processes responsible for the Thatcher illusion are unique to humans. Subsequent studies suggest, however, that other monkey species indeed perceive the Thatcher illusion. Nakata and Osada (2012) trained squirrel monkeys (*Saimiri sciureus*) to distinguish a target face from a distractor face in a two forced choice (2FC) discrimination task. The squirrel monkeys were less sensitive to Thatcherization when the stimuli were presented upside down, and the authors concluded from this observation that squirrel monkeys experience the Thatcher illusion. Studies that use passive-viewing paradigms have revealed evidence for the Thatcher illusion in rhesus macaques (*Macaca mulatta*) (Adachi et al. 2009; Dahl et al. 2010). Adachi et al. (2009), for example, habituated rhesus monkeys to several unaltered conspecifics' faces and then demonstrated increased looking time, dishabituation, when these faces were Thatcherized and presented in their upright orientation, but not if the Thatcherized faces were presented in their inverted orientation. They conclude that rhesus monkeys have increased sensitivity to the Thatcher illusion in upright faces. Dahl et al. (2010) used a similar habituation–dishabituation paradigm and confirmed that rhesus monkeys dishabituated to upright Thatcherized rhesus monkey faces, but not to inverted Thatcherized rhesus monkey faces. Interestingly, the rhesus monkeys failed to show the same sensitivity to upright Thatcherized human faces following habituation to unaltered upright human faces, despite the fact that the monkey subjects in this study had experience in viewing many human faces. This result suggests that the Thatcher illusion may be more likely to be seen in conspecifics' faces. It is unclear whether the discrepancy between the results of Parron and Fagot's (2008) study and Nakata and Osada's (2012) study is a result of the differing testing procedures or whether they are due to genuine differences in the cognitive abilities of the species tested. These inconsistencies are typical of the comparative face-processing literature (Leder et al. 2001) and make it difficult to draw definitive conclusions regarding similarities or differences in these skills across species. Our approach has been to use a simple two-choice discrimination task, matching-to-sample (MTS), to compare the face-processing abilities of both chimpanzees and rhesus monkeys (Parr 2011b; Parr et al. 2006, 2008). In particular, chimpanzees are our closest living relatives and serve as a valuable comparison species for testing human cognitive specializations. In these studies, we have demonstrated many similarities between the face-processing skills of chimpanzees and humans, but notable differences for macaques (Parr 2011a). Our previous studies have demonstrated that both chimpanzees and rhesus monkeys reliably show inversion effects for conspecifics' faces (Parr et al. 1998, 1999, 2008; Parr 2011b).

Here, we tested the ability of chimpanzees and rhesus monkeys to discriminate between unaltered and Thatcherized conspecifics' faces presented in their upright and inverted orientation in a two-choice MTS task. Two previous studies have revealed the Thatcher illusion in rhesus macaques (Adachi et al. 2009; Dahl et al. 2010); this species is included here to strengthen those results using a different testing protocol. Performance-based paradigms are prevalent in studies investigating the Thatcher illusion in humans and have previously revealed the perception of the Thatcher illusion in a nonhuman primate species (Nakata and Osada 2012). Importantly, all of our rhesus monkey and chimpanzee subjects had extensive exposure to face matching tasks using our MTS procedures, and therefore, no additional training was required for this study. Neither species had any experience with the Thatcher illusion prior to this experiment, which allowed us to make direct comparisons about the face-processing capabilities of each species. We hypothesized that chimpanzees would show the Thatcher illusion: Specifically, they would reliably discriminate between an upright Thatcherized face and an upright unaltered face, but not if these stimuli were inverted. Considering that passive-viewing tasks have revealed that rhesus monkeys perceive the Thatcher illusion (Adachi et al. 2009; Dahl et al. 2010), we anticipated that the rhesus monkeys would be able to discriminate between upright Thatcherized and upright unaltered faces in the MTS paradigm used here.

Methods

Subjects

Five chimpanzees (*Pan troglodytes,* three males and two females, 15–22 years old) and six rhesus monkeys (*M. mulatta,* two males and four females, 9–10 years old) participated in this study. The chimpanzees were captive born at Yerkes National Primate Research Center and reared by humans in peer social groups. The monkeys were raised in large social groups at the Yerkes field station (Lawrenceville, Georgia) prior to being relocated to the

Yerkes main station (Atlanta, Georgia) at 3–4 years of age. All subjects were familiar with the computerized MTS procedures used here and had previously completed tasks that required them to discriminate between faces (Parr et al. 1998; Taubert and Parr 2009). Water was available ad lib and no food restriction procedures were employed. All procedures used in this study were approved by the Institutional Animal Care and Use Committee of Emory University.

Stimuli

All stimuli presented in this study showed adult female conspecifics' faces with neutral expressions. The images were preprocessed by cropping to show only the head, resizing to 350 pixels in height, and the pupils aligned on the horizontal axis to standardize orientation. The background information in each photograph was covered with a black mask. Stimuli used in trials where the subjects were required to discriminate between individuals (hereafter referred to as "identity discrimination trials") showed different individuals than those presented in the experimental trials, where subjects discriminated between manipulations of the same face. All stimuli were presented in color.

Procedures

The subjects were tested voluntarily in their home cages with a computerized MTS procedure. At the beginning of each trial, subjects were required to orient to a sample image centered at the top of the screen. To do this, the chimpanzees moved a joystick-controlled cursor over the image, and the rhesus monkeys were required to touch the sample image three times in rapid succession using a touchscreen interface (Parr et al. 2008). Immediately following this response, two probe images appeared simultaneously on the opposite side of the screen, equidistant from the sample. We anticipated the experiments would be difficult for both species, so the sample image was programmed to remain onscreen following orientation to make the task easier and to avoid problems associated with floor performance. A correct response was recorded when the individual selected the image that matched the sample. Correct responses were rewarded with food delivery and a one-second inter-trial interval, while incorrect responses were not food rewarded and were followed by an eight-second inter-trial interval. Chimpanzees additionally received computerized auditory feedback for correct and incorrect responses (a high- or low-pitched tone, respectively). The experimental and identity discrimination trials were presented randomly in each testing session.

Experiment 1: Thatcher Illusion

In Experiment 1, all three images in an experimental display, sample, target, and foil, were derived from one photograph of an individual. The Thatcher illusion was created by inverting the eyes and mouth 180 degrees (see Fig. 1a for illustration on a chimpanzee face). In a given session, the faces of nine conspecifics were presented in one of the four conditions: upright unaltered, upright Thatcherized, inverted unaltered, and inverted Thatcherized (Fig. 1a, b). In the upright unaltered condition, the matching pair showed identical upright, unaltered images, while the foil was the Thatcherized version of the same picture. In the upright Thatcherized condition, the sample and correct match were Thatcherized faces, while the foil was upright and unaltered. The upright Thatcherized condition was included to confirm that subjects were matching-to-sample and not merely biased toward choosing unaltered images. We simply inverted all the images in each experimental trial to create the two additional conditions: an inverted unaltered condition and an inverted Thatcherized condition.

The conditions were blocked so that the subjects were presented with a single condition in each experimental session, and each subject was required to complete four sessions of each condition for a total of 16 sessions. The order of conditions was counterbalanced across subjects and the order of conditions was randomized within subjects. For each condition, the nine unique trials were repeated twice, totaling 18 experimental trials per session. In order to motivate the subjects to complete the task while continuously encouraging a face-processing strategy, we included 32 identity discrimination trials in each session. Thus, each subject was required to complete 50 trials in each session. In all of the identity discrimination trials, the correct pair showed identical, upright faces and the foil was another female's face.

The results for Experiment 1 showed that, counter to prediction, the rhesus monkeys had difficulty with all four experimental conditions. Previous research shows rhesus macaques are capable of perceiving the Thatcher illusion (Adachi et al. 2009, Dahl et al. 2010), so we designed three follow-up experiments in an attempt to account for their performance here.

Follow-up Experiments

Inner Thatcher

In the stimuli used for Experiment 1, the features surrounding the face such as ears, the crown of the head, and cheeks were left intact (Fig. 1b). In this follow-up experiment, we replicated the Thatcher experiment designed for

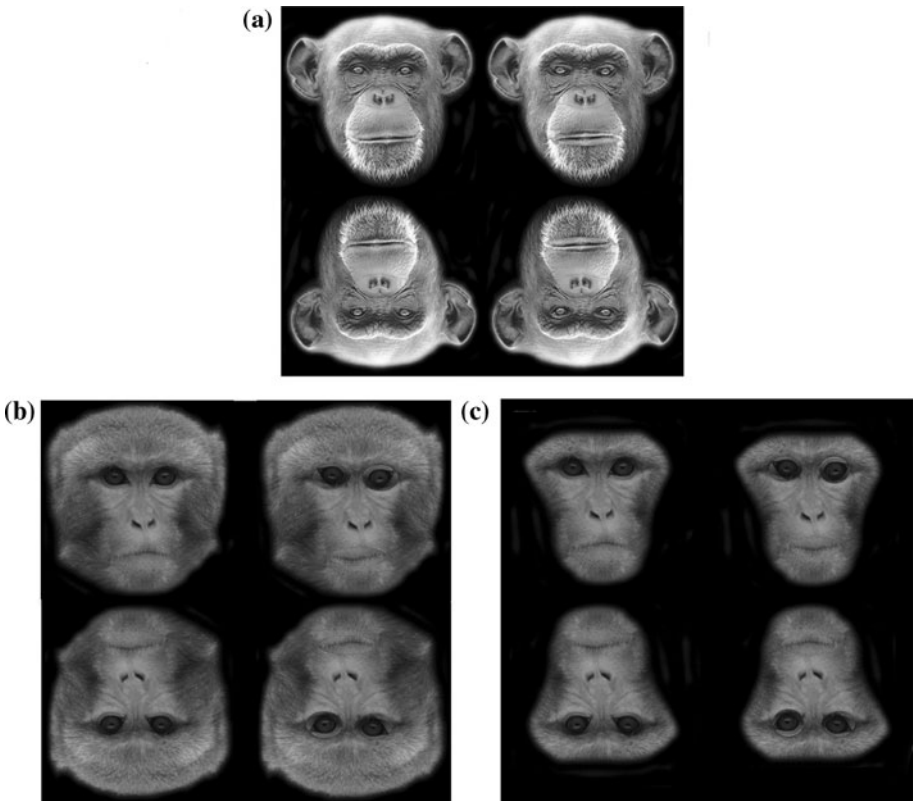

Fig. 1 Examples of Experiment 1: Thatcher Illusion manipulations in a chimpanzee face (Fig. 1a) and a rhesus monkey face (Fig. 1b). In the Thatcherized images, the eyes and mouths have been rotated 180 degrees. Each panel of faces shows the four conditions of the sample images: the upright unaltered face (*upper left*), upright Thatcherized (*upper right*), inverted unaltered (*lower left*), and inverted Thatcherized (*lower right*). Figure 1c illustrates the Thatcher manipulation applied to a rhesus monkey face excluding external features, as described in Follow-up "Experiment 1": Inner Thatcher

the rhesus monkeys, but further manipulated the experimental stimuli by masking those "external features" and leaving only the inner facial features, including the eyes, nose, and mouth (Fig. 1c). This manipulation was similar to the type of cropping performed on the face stimuli by Dahl et al. (2010) who reported positive evidence for the Thatcher illusion in rhesus monkeys using passive-viewing tasks. These authors removed all cues related to external features, and the close circular cropping around the face might have biased subjects' attention to changes in the orientation of the inner features. Each session in our experiment consisted of nine experimental trials repeated twice and 32 identity discrimination trials for a total of 50 trials. The stimuli used for the identity discrimination trials in this experiment were unaltered from Experiment 1.

Feature Manipulation

If the rhesus monkeys use more low-level cues to differentiate between faces, it is possible that the Thatcher manipulation was too subtle for the subjects. Essentially, the monkeys may have been insensitive to the Thatcher manipulation in light of the global similarity (being the same identity) between the target and foil. This experiment was designed to test whether the rhesus monkeys would discriminate between globally similar faces with local feature manipulations that were more apparent than simply inverting the eyes and mouth. As in Experiment 1, all three stimuli in an experimental display were derived from the same photograph. We used the faces of nine monkeys that were not used in Experiment 1 for stimuli and manipulated local features by placing red stars over the pupils of the sample and target faces. The incorrect choice was the same photograph with blue squares superimposed over the pupils (Fig. 2). The single session consisted of nine experimental trials repeated twice and 32 identity discrimination trials for a total of 50 trials. Trials were counterbalanced across individuals and randomized within individuals as in the previous experiments.

Whole Face and Internal Features

This experiment was also applied only to the rhesus monkeys. In this experiment, the monkeys were asked to discriminate between identities rather than between two manipulations of the same monkey face. We used four conditions (whole face, internal features only, mixed condition one, and mixed condition two) to explore the importance of external features in identity discrimination by rhesus monkeys (Fig. 3). In the whole face and internal features only conditions, the monkeys were required to match different photographs of the same monkey, while the incorrect choice showed a different individual. In the whole face condition, the features surrounding the face such as

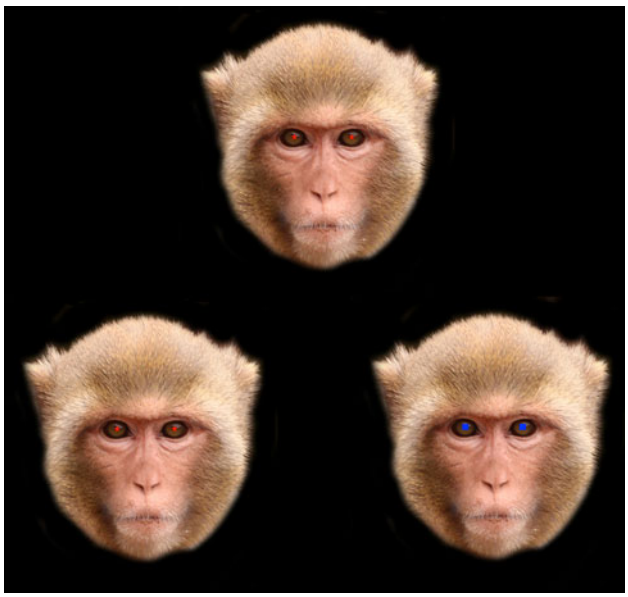

Fig. 2 An illustration of the stimuli used in the Follow-up Experiment II: Feature Manipulation. All three images show the same face. The correct pair of faces is indicated by stars over the pupils, while the foil has *squares* over the pupils. All stimuli were presented in color. The stars were always colored *red* and the *squares* were always colored *blue* (color figure online)

ears, the crown of the head, and cheeks were left intact (Fig. 3b). In the internal features only condition, we masked those "external features" and left only the internal facial features, including the eyes, nose, and mouth (Fig. 3a). The cropping in the internal features only condition was done in the same manner described in Follow-up Experiment I: Inner Thatcher.

In mixed condition one and mixed condition two, the sample and target showed the same individual but mixed whether that individual was represented by its whole face or by internal facial features only. The foil showed a different individual's face composed in a way that matched the sample. In mixed condition one, for example, the sample face showed only the internal features of Monkey A, while the correct match was the same photograph of Monkey A, including the external features, for example, ears, cheeks, etc. The foil face showed only the internal features of Monkey B (Fig. 3c). In mixed condition two, the sample face showed the whole face of Monkey A, while the correct match was the same photograph of Monkey A but showing only the internal features. The foil face showed the whole face of Monkey B (Fig. 3d). The four conditions were blocked so that the subjects were presented with a single condition in a session. The order of conditions was programmatically randomized across subjects. Each subject completed a single session of each condition.

We used photographs of six conspecifics to create the stimuli in this study. Each of the six identities was used as a sample in each condition and as a foil for each of the five other identities, which totaled 30 experimental trials per condition. Simple identity discrimination trials as described in Experiment 1 and Follow-up Experiments I and II were not included in this experiment.

Data analysis

Because no suitable nonparametric tests were available given our small sample sizes, we used parametric statistics for the overall analysis in Experiment 1 and Follow-up Experiment I. This assumes a normal distribution for these data; however, this assumption was not specifically tested. Data were analyzed using repeated measures ANOVA using sample type (unaltered and Thatcherized) and orientation (upright and inverted) as fixed effects. Subject was included in the model as a random factor. We conducted planned comparisons of the means adjusted for all variables included in the model to test for significant differences.

In Follow-up Experiments II and III and for all identity discrimination trials, we performed binomial tests to determine whether the animals' performance was significantly different from chance (i.e., 50 % correct responses). The subjects' individual P values were combined using Fisher's method, and a single P value is reported where appropriate (Sokal and Rohlf 1995 pp. 794ff.).

Results

Experiment 1: Thatcher Illusion

Chimpanzees

Two-way repeated measures ANOVA performed on the subjects' number of correct responses revealed a main effect of orientation ($F_{1,\ 15} = 51.87$, $P < 0.001$, $\eta^2 = 0.776$). Importantly, there was no indication that sample type (unaltered or Thatcherized) influenced subjects' accuracy ($F_{1,\ 15} = 1.27$, $P = 0.28$, $\eta^2 = 0.078$), nor any evidence of an interaction between sample type and orientation ($F_{4,\ 15} = 1.25$, $P = 0.097$, $\eta^2 = 0.077$). These results suggest that the main effect of orientation was not driven by a general bias against selecting Thatcherized faces.

Pairwise comparison of the adjusted means revealed that the chimpanzees' performance on upright unaltered trials was not significantly different from their performance on upright Thatcherized trials ($P = 0.23$) and their performance on inverted unaltered trials was not significantly different from inverted Thatcherized trials ($P = 0.94$). However, their performance was significantly better on upright unaltered trials than inverted unaltered trials

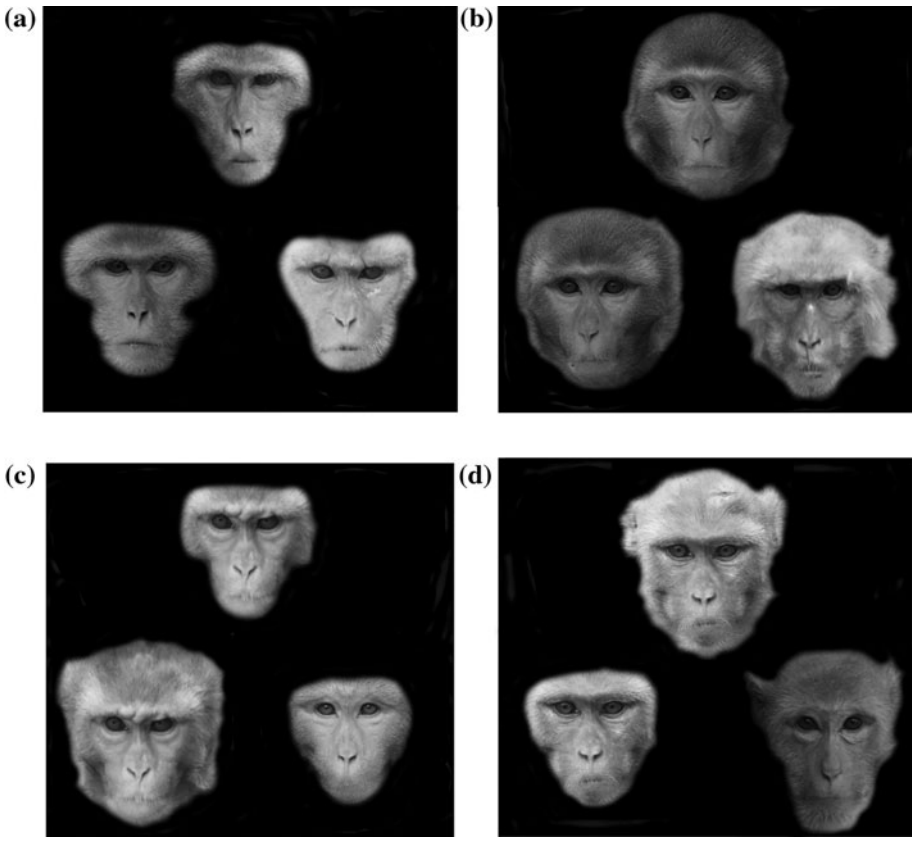

Fig. 3 Examples of the experimental displays for each condition in Follow-up Experiment III: Whole Face and Internal Features. Figure 3a shows the internal features only manipulation in which the correct pair of faces shows two photographs of the same individual and the foil shows the internal features of a different monkey. Figure 3b shows the same conditions for whole face condition, where the external features of the face were left intact. Figures 3c, d reflect the manipulations for mixed condition one and mixed condition two, respectively. For both conditions, the correct pair shows the same photograph with different manipulations, and the foil shows a different individual with the same feature manipulation as the sample. Figure 3c reflects an experimental display in mixed condition one, wherein the rhesus monkeys were required to match the internal features to a whole face. Figure 3d illustrates mixed condition two, where the subjects were required to match a whole face to a face including only internal features

($P = 0.006$). The chimpanzees also performed significantly better during the upright Thatcherized trials compared to the inverted Thatcherized trials ($P < 0.001$; Fig. 4). This result is consistent with the Thatcher illusion. Importantly, the subjects performed significantly above chance for identity discrimination trials ($P < 0.001$, two-tailed binomial test).

Rhesus Monkeys

Two-way repeated measures ANOVA performed on subjects' accuracy did not reveal a significant effect of orientation ($F_{1,\ 18} = 0.009$, $P = 0.93$, $\eta^2 < 0.001$). Instead, there was a main effect of sample type ($F_{1,\ 18} = 20.53$, $P < 0.001$, $\eta^2 = 0.53$). The monkeys performed more accurately when the task required them to match two unaltered faces than two Thatcherized faces ($P < 0.001$). Though the rhesus monkeys' performance on upright unaltered trials was significantly better than their

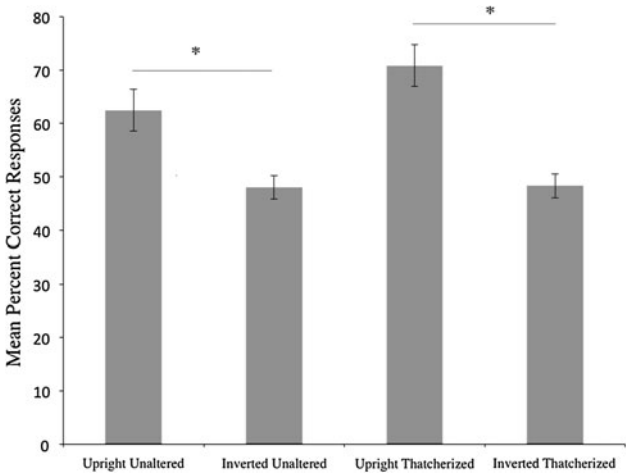

Fig. 4 Mean performance (% correct) for chimpanzees matching unaltered or Thatcherized comparison faces to an identical sample in each orientation condition. *Asterisks* indicates that performance between indicated conditions were significantly different from each other ($P < 0.05$). *Error bars* represent standard errors

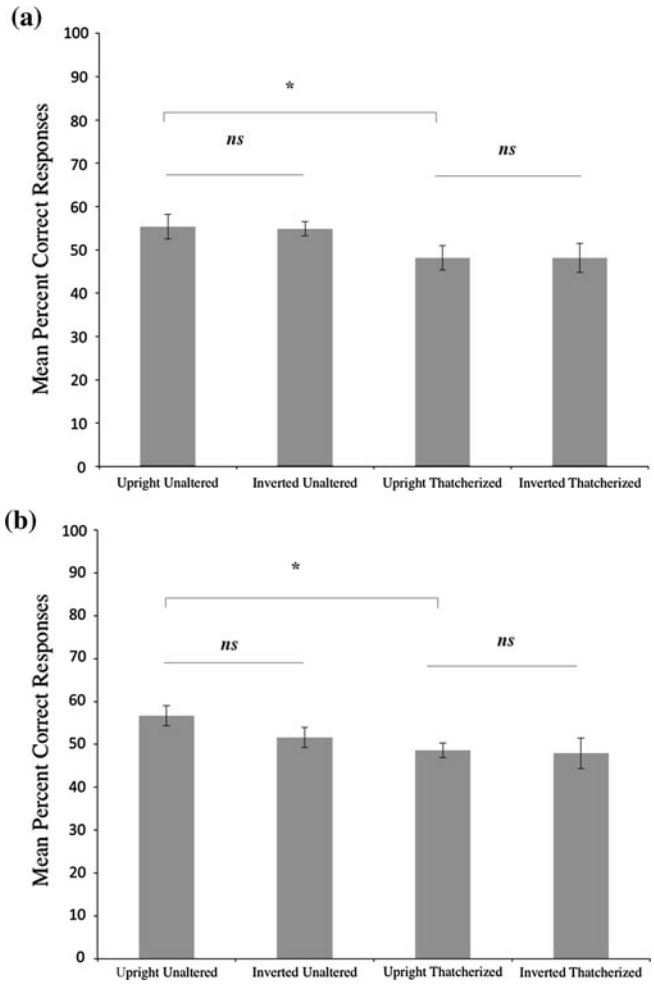

Fig. 5 Mean performance (% correct) for rhesus monkeys matching unaltered or Thatcherized comparison faces to an identical sample in each orientation condition. Figure 5a shows the rhesus monkeys' performance in Experiment 1: Thatcher Illusion, where external features of the stimuli were intact. Figure 5b shows the rhesus monkeys' performance in Follow-up Experiment I: Inner Thatcher, where the stimuli were cropped to show only the internal features of the monkey faces. Significant differences in performance between conditions ($P < 0.05$) are marked by an *asterisk*. *Error bars* represent standard errors

performance on upright Thatcherized trials ($P = 0.012$; Fig. 5a), their performance on upright unaltered trials was not significantly better than on inverted unaltered trials ($P = 0.88$). Additionally, their performance on upright Thatcherized trials did not differ from their performance on inverted Thatcherized trials ($P = 1.00$). Taken together, these data do not indicate that the rhesus monkeys experienced the Thatcher illusion in these trials. Subjects also performed significantly above chance for identity discrimination trials ($P < 0.0001$, two-tailed binomial test).

Follow-up Experiments

Inner Thatcher

A two-way repeated measures ANOVA on subjects' performance failed to reveal a significant main effect of orientation ($F_{1,\ 18} = 2.03$, $P = 0.17$, $\eta^2 = 0.101$); nor was there a significant interaction between sample type and orientation ($F_{5,\ 18} = 0.78$, $P = 0.38$, $\eta^2 = 0.043$). There was, however, a significant effect of sample type ($F_{1,\ 18} = 4.59$, $P = 0.046$, $\eta^2 = 0.20$) in that the monkeys performed significantly better on the unaltered compared to the Thatcherized trials.

Pairwise comparisons of the adjusted means revealed that the rhesus monkeys' performance on upright unaltered trials was, again, significantly better than their performance on upright Thatcherized trials ($P = 0.043$). However, their performance on upright unaltered trials was not significantly better than on inverted unaltered trials ($P = 0.11$). Additionally, their performance on upright Thatcherized trials did not differ from their performance on inverted Thatcherized trials ($P = 0.84$). There was no difference in performance on the inverted unaltered and inverted Thatcherized trials ($P = 0.33$; Fig 5b). These data do not support the presence of the Thatcher illusion in rhesus monkeys.

The rhesus monkeys performed significantly above chance for the identity discrimination trials ($P < 0.001$, two-tailed binomial test).

Feature Manipulation

A binomial test demonstrated that the monkey subjects' did not perform above chance for the experimental trials

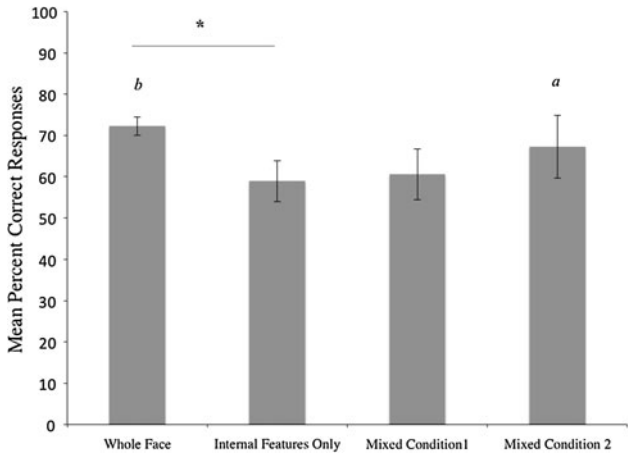

Fig. 6 Mean performance (% correct) for rhesus monkeys discriminating faces in Follow-up Experiment III: Whole Face and Internal Features. Here, the letter "*a*" indicates conditions for which performance was significantly above chance ($P < 0.05$; two-tailed binomial test). The letter "*b*" indicates conditions for which performance showed a trend toward above chance performance ($P = 0.056$; two-tailed binomial test). The *asterisk* indicates significant differences in performance between conditions ($P < 0.03$; paired *t* test). *Error bars* represent standard errors

($P = 0.999$, two-tailed) but did perform above chance in the identity discrimination trials ($P < 0.001$, two-tailed). These results for the experimental trials indicate that the colored shapes superimposed over the pupils in the experimental stimuli did not influence the rhesus monkeys' behavior.

Whole Face and Internal Features

Binomial tests on the monkeys' accuracy demonstrated a trend toward above chance performance in the whole face condition ($P = 0.056$, two-tailed). In contrast, the rhesus monkeys did not perform above chance in the internal features only condition ($P = 0.71$, two-tailed; Fig. 6). A paired *t* test demonstrated that performance discriminating the whole face trials was significantly better than performance discriminating internal features only trials ($t_5 = 2.93$, $P < 0.03$). These results support the conclusion that the external features of the monkey faces carry important information about identity.

The subjects did not perform above chance on mixed condition one (internal features only sample matched to whole face; $P = 0.39$, two-tailed binomial test). However, binomial tests revealed the monkeys performed above chance on mixed condition two trials (whole face sample matched to internal features only; $P = 0.035$, two-tailed; Fig. 6), indicating that the inclusion of external features aided the monkeys' ability to accurately match conspecifics' faces based on their identity.

Discussion

We used a series of performance-based tasks to investigate the Thatcher illusion in several species of nonhuman primates. This approach yielded the first evidence of the Thatcher illusion in chimpanzees. The chimpanzees reliably discriminated between unaltered and Thatcherized faces when the stimuli were presented upright, whereas performance was impaired when the stimuli were inverted. There is no evidence that this effect was due to a general bias against selecting the Thatcherized faces, as the chimpanzees performed equally well regardless of whether they were required to match Thatcherized faces or unaltered faces (Fig. 4).

In contrast, this study failed to support evidence of a Thatcher illusion in rhesus monkeys. The follow-up experiments with the rhesus monkeys indicate that the presence of external facial features in stimuli might be important when measuring face discrimination in this species. Although the presence (Experiment 1: Thatcher Illusion) or absence (Follow-up Experiment I: Inner Thatcher) of external features did not result in a Thatcher effect (Fig. 5a, b) for rhesus monkeys, we found a trend that suggests that that the monkeys were able to match individual faces across images when external information was present (Follow-up Experiment III: Whole Face and Internal Features). This is a compelling demonstration of a possible bias toward external features. In contrast, human research has shown a bias toward internal features. For humans, removing external information, such as ears and hair, does not affect performance (Hancock et al. 2000; Burton et al., 2005). For this reason, future research should take this information into account when cropping monkey faces because the diagnostic information might not be found were we expect based on our own experience, or human research.

The results of Follow-up Experiment II: Feature Manipulation are consistent with the notion that rhesus monkeys may be less sensitive to subtle manipulations of internal facial features. The rhesus monkeys performed at chance in the trials where salient changes were made to faces (i.e., colorful geometric shapes were superimposed on pictures of rhesus monkeys). Collectively, Follow-up Experiments I and II indicate that the behavior of rhesus monkeys is unlikely to be influenced by subtle manipulations of internal facial features.

This result is at odds with two previous studies of the Thatcher illusion in rhesus monkeys that used passive-viewing procedures. Adachi et al. (2009) hand coded the amount of time four rhesus monkeys spent looking at faces in a habituation/dishabituation paradigm. The stimuli were unmasked, uncropped, and unfamiliar conspecifics' faces presented centrally on a monitor. The rhesus monkeys were

shown ten images (either an upright or an inverted face) in the habituation phase, each for 30 s, followed immediately by a dishabituation phase where the same face and a Thatcherized version of the face appeared twice in an ABBA sequence. In this experiment, looking time in the dishabituation phase was used as a proxy for perceived similarity (Adachi et al. 2009). In both the upright and inverted conditions, the monkeys dishabituated more to the novel Thatcherized face than the unaltered face, but this was greater in the upright condition, indicating that the rhesus monkeys perceived the Thatcherized version of the inverted face as more similar to the unaltered inverted face. Dahl et al. (2010), on the other hand, removed all external features (head contour and ears) from human and rhesus monkey faces and recorded looking time with an eye-tracker using a slightly different version of a habituation/dishabituation paradigm. Instead of reporting looking duration (Adachi et al. 2009), these authors reported the rebound (i.e. the net difference between looking time in the dishabituation compared to habituation trials). They found greater "rebound of interest" for the upright trials compared to the inverted trials, implying that the perceived difference between the unaltered and Thatcherized faces was affected by orientation (Dahl et al., 2010). However, we are unable to support these previous findings using a performance-based task.

One possible reason for this result is that the monkeys were responding to the MTS task using a strategy that did not rely on the face-processing system. Although we observed a high level of proficiency in Follow-up Experiment III, in which the same subjects were asked to match facial identity in different photographs, suggesting that these rhesus monkeys were not simply matching low-level, image-based properties, it is impossible for us to know exactly what the subjects are matching in a training task such as this. However, in the past, a number of studies have used the MTS procedure to successfully measure other face discrimination phenomena in this species (for a summary see Parr 2011a, b), and we were able to find evidence of a Thatcher effect when we tested chimpanzees with this same procedure.

Another possibility is that the behavioral protocol employed here is not sensitive enough to reveal the Thatcher illusion in rhesus monkeys. Nakata and Osada (2012) were successful in revealing the Thatcher illusion in squirrel monkeys with a performance-based task, but their task included a training phase where the subjects learned over several sessions to distinguish between unaltered and Thatcherized faces, whereas our subjects had no prior experience with Thatcherized faces. The two previous studies that found the Thatcher illusion in rhesus monkeys (Adachi et al. 2009, Dahl et al. 2010) used untrained passive-viewing tasks under more controlled conditions (i.e., in a darkened, sound-attenuating booth), whereas our subjects were tested in their home cages and participation was voluntary. Given that the subjects in this experiment had visual and auditory exposure with other rhesus monkeys in the room during testing, environmental factors may have reduced the rhesus monkeys' attention to subtle feature manipulations.

The procedure reported by Dahl et al. (2010) was gaze contingent in that subjects were required to fixate on the monitor in order to initiate the stimulus presentations, and Adachi et al. (2009) used direct gaze as the dependent measure, both to demonstrate habituation and to calculate dishabituation. These authors both argue that their passive-viewing procedures are free of any trained response biases that could affect the performance of the subjects and that these issues might explain some of the reported species differences in face processing between rhesus monkeys and humans (Parr 2011a, b), similar to what we are reporting here. However, the rhesus monkeys would have still needed training to fixate on a screen, and if the location for fixation training happened to be toward the top of the experimental stimulus, then it is possible that the subjects would be more likely to notice local changes made to faces when presented upright than when presented upside down. Furthermore, fixation training in general might interact with and influence face discrimination processing. For example, if fixation training directs attention toward internal facial features, then face discrimination processing in rhesus monkeys might be masked in fixation tasks.

The comparative aspect of this paper is important because it examines two nonhuman primate species rather than comparing the performance of one nonhuman species to human performance. Comparisons between nonhuman species are, in some ways, more informative because both species can be tested without the benefit of language and verbal instruction. Thus, the fact that our initial Thatcher experiment yielded a positive result in one species and not the other suggests that there might be genuine discontinuity in face processing across primate species. Thus, after years of research, there is still some debate as to whether monkeys possess the same cognitive specializations for discriminating faces as chimpanzees and humans. Importantly, future cognitive studies of nonhuman subjects should carefully consider all aspects of methodology and stimulus preparation when designing experiments.

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Conflict of interest None.

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