# A comparative study of face processing using scrambled faces

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**Abstract.** It is a widespread assumption that all primate species process faces in the same way because the species are closely related and they engage in similar social interactions. However, this approach ignores potentially interesting and informative differences that may exist between species. This paper describes a comparative study of holistic face processing. Twelve subjects (six chimpanzees *Pan troglodytes* and six rhesus monkeys *Macaca mulatta*) were trained to discriminate whole faces (faces with features in their canonical position) and feature-scrambled faces in two separate conditions. We found that both species tended to match the global configuration of features over local features, providing strong evidence of global precedence. In addition, we show that both species were better able to generalize from a learned configuration to an entirely novel configuration when they were first trained to match feature-scrambled faces compared to when they were trained with whole faces. This result implies that the subjects were able to access local information easier when facial features were presented in a scrambled configuration and is consistent with a holistic processing hypothesis. Interestingly, these data also suggest that, while holistic processing in chimpanzees is tuned to own-species faces, monkeys have a more general approach towards all faces. Thus, while these data confirm that both chimpanzees and rhesus monkeys process faces holistically, they also indicate that there are differences between the species that warrant further investigation.

**Keywords:** visual cognition, evolutionary psychology, animal behavior, nonhuman primates, holistic processing, face discrimination

## 1 Introduction

A large body of research suggests that we have a highly selective neural network to process face stimuli (for a review see Tsao and Livingstone 2008). Conventional wisdom has assumed continuity across the primate order, because the recognition of individual faces is thought to support social behavior, and all primates are considered social. However, our ability to discriminate and recognize faces is known to differ according to experience with particular groups (species: Pascalis et al 2002; races: Hayward et al 2008; Meissner and Brigham 2001; Michel et al 2006a, 2006b) and familiarity with individuals (Bruce and Young 1986; Bruce et al 1999; Megreya and Burton 2006). The formation of social out-groups also seems to play a crucial role in the application of these skills (Bernstein et al 2007). The aspects of face processing that are highly conserved across species are thus likely to be masked by individual development in Western adults. Recent comparative research, which has reported gross similarity across species, has also suggested that there are potential differences in the way different primate species respond to faces (Parr et al 2008; Parr and Taubert 2011; Taubert and Parr 2009, 2011). If we could isolate all of these differences, we would be in a position to understand the development and evolution of face processing in humans.

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In this study we are interested in an aspect of face perception that has attracted a lot of attention in the human literature, namely holistic processing (for reviews see McKone et al 2007; Rossion 2008). According to the holistic processing hypothesis, a face is processed as a whole rather than a collection of smaller features (Davidoff and Donnelly 1990; Sergent 1984). Empirical support for this hypothesis comes from studies that have shown humans are more sensitive to global information than local features providing a face is upright (Tanaka and Farah 1993; Young et al 1987; for a review see McKone et al 2007). Holistic processing is likely to be conserved across species because it develops early in infancy (Turati et al 2002); however, it is also tuned by experience. In 2006 Michel et al used the part–whole effect (adapted from Tanaka and Farah 1993) to demonstrate that holistic processing was reduced for other-race faces, when compared to own-race faces (also see Hayward et al 2008). In a related study, Michel et al (2006) reported that the composite face effect, another marker of holistic processing (see Young et al 1987), was greater for own-race than other-race faces. Taken together these studies suggest that we process own-race faces more holistically than other-race faces because we have more experience with own-race faces.

While a large number of studies have tested holistic processing in humans, it has been investigated in nonhuman primates only a few times. In 2007, Dahl et al modified the composite-face task and found evidence that rhesus monkeys perceive faces as Gestalts using reduced looking preference in a habituation/dishabituation paradigm as a proxy for accurate recognition. However, the question of whether holistic processing was reduced for unfamiliar categories of faces, for example other-species faces, remained open to speculation. Later, in 2009, Taubert and Parr also tested rhesus monkeys and, using a standard match-to-sample (MTS) task, measured the size of the composite-face effect for human faces, chimpanzee faces, gorilla faces, and sheep faces. Based on their results they claimed that experience did not predict the size of the composite-face effect in this species (Taubert and Parr 2009); however, they also failed to include an own-species condition (ie rhesus monkey faces) to serve as an appropriate baseline. More recently, Taubert et al (in press) have used the composite-face effect to directly compare holistic processing in both chimpanzees and rhesus monkeys and found that, while chimpanzees tolerated contrast-reversal (in a similar way to humans—Hole et al 1999), the composite-face effect in monkeys was limited to positive-contrast faces. Again, the subjects were only tested with the faces of their own-species (Taubert et al, in press). An outstanding question, therefore, is whether holistic processing in chimpanzees and rhesus monkeys is reduced for the faces of other species.

Here, we tested chimpanzees and rhesus monkeys with the faces of three species (humans, chimpanzees, and rhesus monkeys) to confirm the presence of holistic processing and to determine whether it is influenced by disproportional experience with own-species faces. Chimpanzees are interesting because they are our closest living relative and, thus, represent the most direct comparison for understanding human cognitive behavioral and neural specializations. Rhesus monkeys, on the other hand, are more distantly related to us but are more frequently used in experiments designed to understand human cognitive behavioral and neural specializations. First, we trained six chimpanzees and six monkeys to discriminate a set of whole faces at the individual level. Each training trial began with the presentation of a sample face. After subjects made an orienting response towards the sample, they were presented with a choice of two faces (a target and a distractor). Subjects were required to reliably select the target (determined by an 85% performance criterion) before we tested whether they preferred to match the global arrangement of features or the features themselves by measuring subject accuracy after selectively manipulating the arrangement of features in either the distractor (congruent trials) or the target (incongruent trials; see figure 1).
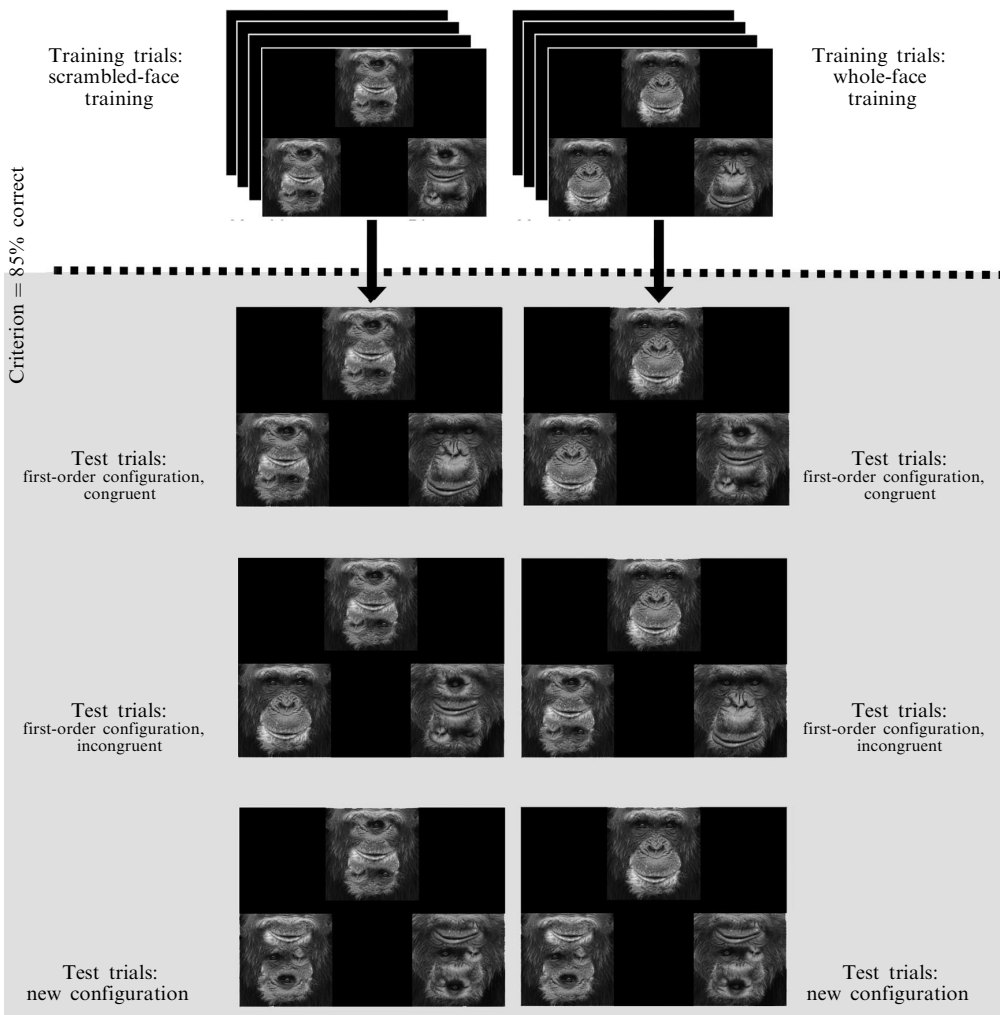
**Figure 1.** A schematic representation of the experimental procedure. Subjects would be trained to discriminate between either whole (training condition 1) or scrambled (training condition 2) faces before they completed corresponding test phase. For the purposes of illustration, in each of these samples the same appears at the top of the visual display with the target in the bottom left corner and the distractor in the bottom right corner.

In congruent test trials, the target was identical to the sample while the distractor (a different identity) was presented in a scrambled format and, therefore, differed from the sample at both the global and local level (see figure 1). The incongruent trials, on the other hand, presented subjects with a feature-scrambled target and a distractor with features in the same global configuration as the sample. In these trials, to correctly match the sample it was necessary for subjects to ignore the arrangement of features and diagnose identity on the basis of local details (see figure 1). A subsequent increase in error would suggest that global information was interfering with the identity-matching task and that, despite extensive practice matching the sample to the target, the subjects were more likely to select the distractor as the matching stimulus.

You might also predict better performance in the congruent trials if subjects were more likely to select normal faces over unusual scrambled faces. To rule out this explanation, we also tested subjects after they had successfully learned to discriminate between a second set of scrambled faces (see figure 1). In contrast to the congruent

trials that followed whole face training, the congruent trials that followed training with scrambled faces required subjects to match a scrambled face to an identical image, ignoring a distractor with features in the canonical configuration. In the incongruent trials, subjects had to match a scrambled sample to the same identity presented as a whole face, rejecting the scrambled distractor. Thus, a main effect of congruency would be consistent with the subjects matching global information over local details. An interaction between congruency and training condition, however, would indicate that subjects tended to select whole faces (as the more usual stimulus) regardless of the experimental condition.

We also included new configuration trials in the test phase. In these trials a subject was given a sample in the learned configuration (a whole face or a scrambled face) and asked to discriminate between two faces (a target and a distractor) that were presented in an entirely novel configuration (see figure 1). Thus, unlike in the congruency trials where subjects were asked to discriminate between comparison stimuli that differed in their arrangement of features, subjects were asked to discriminate between two comparison stimuli that only differed at the individual level. It was expected that, if whole faces were processed more holistically than scrambled faces, as suggested by the human literature (Collishaw and Hole 2000; Hayward et al 2008; Schwaninger et al 2002; also see Robbins and McKone 2003), then it should be easier for the subjects to generalize from a scrambled configuration to a novel configuration than to generalize from a whole configuration to a novel configuration.

## 2 Method
### 2.1 Subjects
A total of six chimpanzees (*Pan troglodytes*) ranging in age from 15 to 22 years participated in this study. Four subjects were male (Jarred, Lamar, Patrick, and Scott) and two were female (Katrina and Faye). All six chimpanzees were captive born and raised by humans in peer groups at the Yerkes Primate Center nursery (main station, Atlanta, GA) allowing for typical social interactions during development. At 4 years of age they were moved from nursery groups to mixed-age groups housed in adjacent indoor/outdoor enclosures allowing for visual and auditory contact with a large number of neighbors.

The six rhesus monkeys (*Macaca mulatta*) that served as subjects were between 8 and 9 years old at the time of testing. Two of the monkeys were male (Rk7 and Sm7) and four were female (On8, Oi8, Cw7, and Lm7). All monkeys were reared in large social groups at the Yerkes field station (Lawrenceville, GA) before being relocated to the Yerkes main station at 3 years of age. At the main station they were pair-housed in a large colony room housing approximately 12 other rhesus monkeys that were not participating in this study.

At the time of testing, all twelve subjects had previously demonstrated the ability to correctly match individual faces (and other kinds of objects) in the match-to-sample paradigm over many years (for examples of previous experiments see Parr et al 1998, 2000, 2006, 2008; Parr and Taubert 2011; Taubert and Parr 2009, 2011). Five of the chimpanzees (three males and one female) tested in this study were also tested by Hopkins and Washburn in their 2002 study of global-to-local processing.

### 2.2 Visual stimuli
In this paper the nonhuman faces were digital photographs taken of 24 chimpanzees and 24 monkeys that were unfamiliar to the subjects. The 24 human faces were photographs taken from the Caltech human face (front) dataset collected by M Weber (http://www.robots.ox.ac.uk/~vgg/data3.html). Photographs were converted to 256 shades of gray (luminance and contrast were adjusted manually to minimize overall differences),

and background information was replaced with a black mask. Images were then pre-processed to ensure approximate image scaling ($600 \times 600$ pixels) and feature placement with faces aligned according to their line of horizontal symmetry; however, to preserve the images as naturalistic as possible no further editing was performed, and thus hair and other asymmetries were tolerated within the images.

These whole-face stimuli were scrambled in a two-step process using the Psycho-physics Toolbox extensions (Brainard 1997; Pelli 1997) in a Matlab (v 7.8) environment. The first step rearranged the location of the four feature locations. The second step rearranged the vertical relationship between features. To avoid the introduction of high-frequency borders, features were scrambled using a flattened Gaussian subtraction/ addition method as opposed to a direct replacement of the pixels. Essentially, pixels were smoothly removed from an area on the image and then replaced. This technique ensured a smooth transition from the features to surrounding face, producing scrambled faces with significant differences in their global information without the introduction of salient borders surrounding features. Of all the possible feature combinations that could be produced using this technique only three were necessary for the experiment: whole faces (two eyes, above a nose, above a mouth), scrambled faces (left eye, above a mouth, above a nose paired with the right eye), and new configuration faces (a mouth, above the right eye paired with a nose, above the left eye). These particular combinations of features were selected because all features were displaced from their typical positions, and because the left and right eyes were no longer paired together.

### 2.3 Design and procedure

The chimpanzees were tested voluntarily in their home enclosure with a mobile computer cart housing a computer and 19 inch monitor, positioned approximately 40 cm away from the cage mesh. Faces were presented at a standard size of $350 \times 350$ pixels. Responses were collected via a joystick that was attached to the cage mesh. Likewise for the monkeys, testing took place in the subject's home cage using a mobile testing cart equipped with two 15 inch touch screen monitors built into a metal frame. These frames allowed the monitors to be attached to the front of the subject's home cage and left for extended periods of time (for more details about the testing equipment see Parr et al 2008). The experiment employed a standard two-alternative forced choice match-to-sample procedure. This procedure has been described in detail elsewhere (see Parr et al 1998, 2006, 2008). In brief, a trial would begin when a single stimulus (the sample) would appear at the top of the screen. Subjects were first required to contact the sample, using either the joystick to move the cursor (chimpanzees) or their hand (monkeys). After this initializing response was recorded, there was a delay of 500 ms followed by the appearance of two comparison stimuli at the bottom of the screen, equidistant from the central sample (see figure 1). One of these comparison stimuli would be the same face as the sample (the target) and represented the correct response. Whether the target was presented on the left or the right of the sample was determined at random. When this image was selected by the subject a "correct" sound was played. Shortly after the chimpanzees received a squirt of juice while the monkeys received a small food reward delivered via an automatic pellet dispenser. The nonmatching comparison stimulus (the distractor) was a face belonging to the same species but a different individual. The selection of the distractor was recorded as an incorrect response. An "incorrect" sound was played and no reward was given. Incorrect responses were also followed by a 6 s inter-trial interval (ITI) whereas correct responses were followed by a shorter 2 s ITI.

In training condition 1, subjects were trained with a set of 12 scrambled faces. For each session a subject completed, 6 of the 12 faces were randomly selected to serve as targets, the other 6 became distractors. Thus, what was a distractor face for one

session would have appeared as a sample/target face for another session. Training continued until accuracy was greater than 85% in a single training session. The scrambled faces presented as part of this training condition were all fixed in the same configuration. In a single training session, each of the 6 targets appeared 8 times, each time paired with 1 of the 6 distractors selected at random (48 trials in total). Trial order was randomized. Immediately after reaching this high performance criterion, subjects completed 144 test trials in four discrete sessions. Thus, there were 36 trials in each test session (12 congruent trials, 12 incongruent trials, and 12 new-configuration trials; see figure 1). Every target (and distractor) was repeated twice per trial type and as such was seen in each test session a total of 6 times. The trial order for each session was determined at random. This entire procedure was then repeated for three species (chimpanzee faces, monkey faces, human faces) with the order of completion counterbalanced across subjects. Following a lengthy delay, approximately 10–20 days, the same procedure was repeated to collect the data for the second training condition (whole faces). The procedure was identical to the first training condition, except a novel set of 36 faces was used (12 per species) and these were presented in one standard scrambled format during the training phase (see figure 1).

## 3 Results

### 3.1 Congruency trials

Subject accuracy was analyzed in a mixed ANOVA with four factors. The repeat factors were congruency condition (congruent, incongruent), training condition (whole faces, scrambled faces), and stimulus species (chimpanzee faces, monkey faces, human faces). The between-subjects factor was subject species (chimpanzees, monkeys).

The effect of congruency revealed that the subjects were significantly better at matching individual faces in congruent trials than in incongruent trials ($F_{1,10} = 73.42$, $p < 0.001$). Decreased accuracy in the incongruent trials suggests that when the features of the sample and the distractor were presented in the same global configuration, it interfered with the subject's ability to match facial identity. The main effects of training condition and subject species were not significant ($Fs < 1$).

Unexpectedly, the main effect of stimulus species was significant ($F_{1,10} = 9.05$, $p = 0.002$). After the Bonferroni adjustment ($\alpha = 0.05/3$), a series of pairwise comparisons revealed that subjects were significantly better at the congruency task when matching human faces than chimpanzee ($t_{11} = 2.81$, $p = 0.02$) or monkey faces ($t_{11} = 5.73$, $p < 0.001$) and that subjects were just as accurate with chimpanzee and monkey faces ($t_{11} = 0.6$, $p = 0.56$). Thus, the effect of stimulus species was driven by better overall performance in the human-face condition.

There was no evidence that the effect of congruency was changed by training condition ($F_{1,10} = 3.72$, $p = 0.083$; see figure 2a). This was an important result because it suggests that the subjects were not biased by a preference for face-like patterns and that subjects continued to adhere to the trained MTS rule (ie match the sample, whether it is a whole face or a scrambled face).

The species of the subject did not mediate the effect of congruency ($F_{1,10} = 0.15$, $p = 0.7$; see figure 2b). However, the interaction between stimulus species and congruency was significant ($F_{2,20} = 4.85$, $p = 0.02$; see figure 2c). The Bonferroni rule was used to adjust three pairwise comparisons ($\alpha = 0.05/3$) and confirm that there was evidence of a preference for global information in each of the three conditions of stimulus species (chimpanzee faces: $t_{11} = 8.06$, $p < 0.001$; monkey faces: $t_{11} = 4.94$, $p = 0.001$; human faces: $t_{11} = 3.54$, $p = 0.005$). Training conditions did not interact with subject species nor did it interact with the repeat factor, stimulus species. There was also no evidence of an interaction between stimulus species and subject species (all $Fs < 1$).
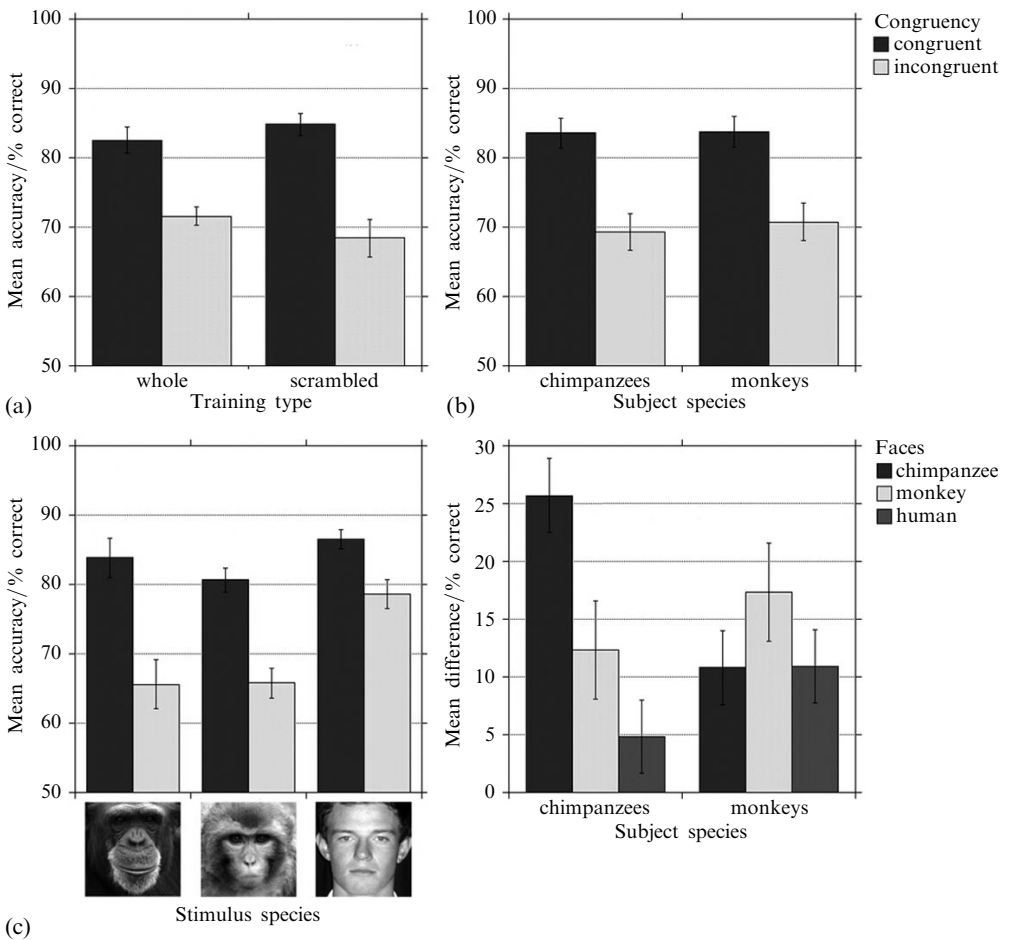
**Figure 2.** (a) The interaction between congruency and training condition (whole faces, scrambled faces); (b) the interaction between congruency and subject species (chimpanzees, rhesus monkeys); (c) the interaction between congruency and the species of stimulus (chimpanzee faces, monkey faces, human faces) with mean matching performance on the $y$ axis; and (d) mean difference in congruency (congruent trials − incongruent trials) as a function of subject species and stimulus species. Error bars = ±1 SEM.

The significant three-way interaction between congruency, stimulus species, and the between-subjects factor, subject species ($F_{2,20} = 6.06$, $p = 0.009$; see figure 2d) justified 6 pairwise comparisons designed to determine the source of this variance ($\alpha = 0.05/6$). We found that chimpanzees tended to match global information over local features when the visual stimuli were chimpanzee faces ($t_5 = 8.02$, $p < 0.001$), but this was not true for monkey or human faces (monkey faces: $t_5 = 2.9$, $p = 0.02$; human faces: $t_5 = 1.54$, $p = 0.15$). Monkeys, on the other hand, were always more likely to choose the comparison stimulus that matched the sample with reference to global configuration regardless of the stimulus species (chimpanzee faces: $t_5 = 3.38$, $p = 0.007$; monkey faces: $t_5 = 4.09$, $p = 0.002$; human faces: $t_5 = 3.47$, $p = 0.006$).

None of the remaining three-way interactions were significant (stimulus species × training × subject species; training condition × congruency × subject species; stimulus species × training condition × congruency; all $F$s < 1). Finally, the interaction between all four factors was also not significant ($F < 1$).

### 3.2 New configuration trials

In these trials, subjects were given a sample in the learned configuration and asked to discriminate between two comparison stimuli that were presented in a novel configuration. If scrambled faces do not activate holistic processing, it was expected that subjects would find it easier to generalize from the learned configuration of features to a novel configuration of features when they learned to discriminate scrambled faces (see figure 1).

The data were analyzed in a $2 \times 3 \times 2$ mixed ANOVA with two repeat factors (training condition and stimulus species) and one between-subjects factor (subject species). Unlike in the congruency trials (see figure 3a), training was found to impact performance in the new configuration trials with subjects better able to generalize from a learned configuration to a novel configuration after acquiring expertise with scrambled faces rather than whole faces ($F_{1,10} = 17.83$, $p = 0.002$; see figure 3b). There was no evidence that the effect of training interacted with stimulus species ($F_{2,20} = 2.05$, $p = 0.15$) or subject species ($F_{1,10} = 1.11$, $p = 0.32$).
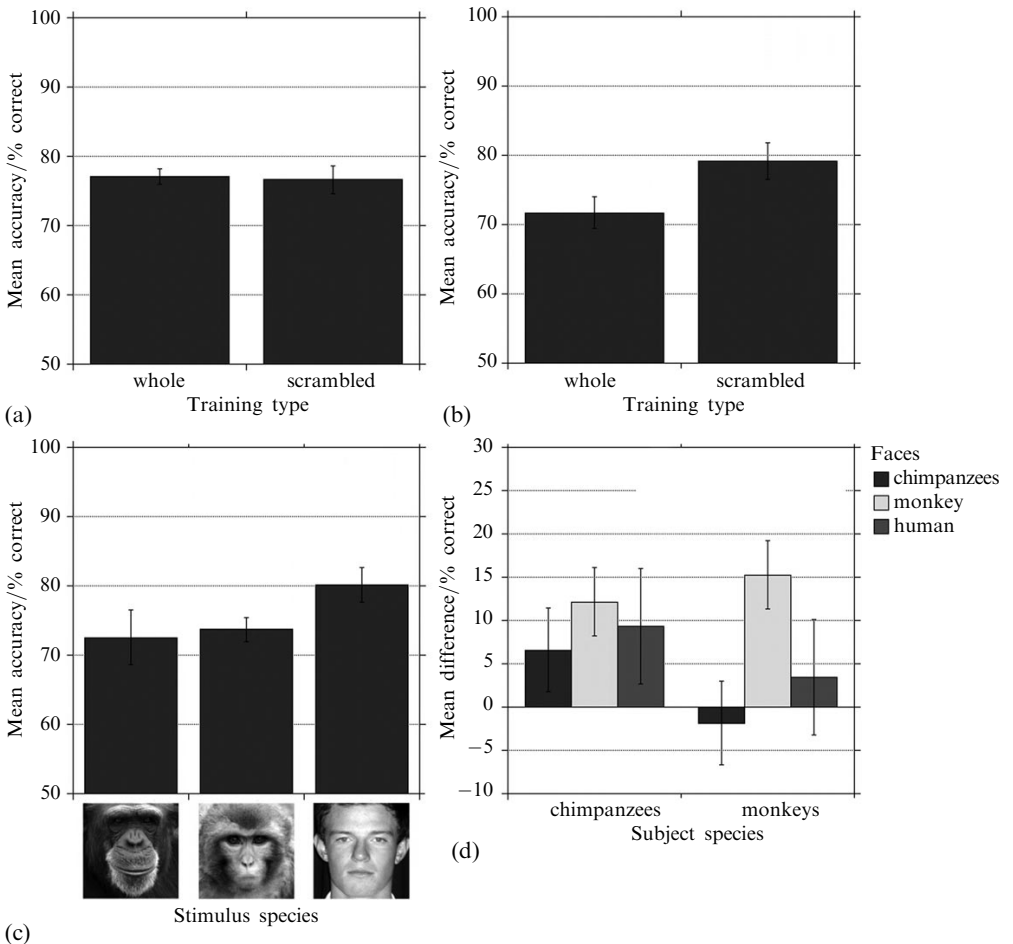


**Figure 3.** (a) The main effect of training type on congruency trials; (b) the main effect of training type on new configuration trials; (c) the main effect of stimulus species; and (d) the mean difference in training condition (scrambled faces − whole faces) for each subject species (chimpanzees and monkeys) separated by stimulus species. Error bars = ±1 SEM.

There was no effect of subject species ($F_{1,10} = 0.14$, $p = 0.72$); however, the species of stimuli was found to have an effect on performance when averaging across the other two factors ($F_{2,20} = 3.85$, $p = 0.04$; see figure 3c). A series of three pairwise tests were used to analyze this effect. After the $\alpha$ level was adjusted for multiple comparisons ($\alpha = 0.05/3$) none of these tests were significant, but subjects tended to be more accurate when matching human faces than when matching chimpanzee ($t_{11} = 2.83$, $p = 0.02$) or monkey ($t_{11} = 2.43$, $p = 0.04$) faces with no evidence of a difference between matching chimpanzee faces and matching monkey faces ($t_{11} = 0.35$, $p = 0.73$). The effect of species did not interact with the between-subjects factor, subject species ($F_{2,20} = 3.27$, $p = 0.06$). The three-way interaction between all three factors in the experimental design was also not significant ($F_{2,20} = 0.57$, $p = 0.57$; see figure 3d).

## 4 Discussion

In this article, we combine cognitive data collected from two species in order to track similarities and differences across the primate order. These current data provide the first compelling evidence that, for both species, global information in faces is registered first and preferentially matched in a discrimination task. The present results are also consistent with the notion that holistic face processing is an obligatory response to the presence of the canonical, whole face, configuration, which pools facial features together into a single unit of analysis. In addition to remarkable similarities, this experiment also uncovered potentially important differences between species that cannot be easily dismissed as the products of methodological variance.

The congruency trials asked subjects to discriminate between two faces that differed at both the holistic (global) and local level. Importantly, subject performance remained high across all test conditions. The implication is that subjects continued to successfully access identity-specific information to perform the trained task, match the identity of the sample face to the target. The subjects simply made more mistakes in the incongruent trials compared to the congruent trials, suggesting that when global structure of the sample and the distractor matched, it interfered with performance but it did not eradicate it. The direction of the difference in accuracy between congruent and incongruent trials is consistent with the notion that subjects preferred to match the arrangement of features, rather than local features.

The data indicate that the effect of congruency interacted with stimulus species. This seems to be largely due to better performance with human faces, which begs the question why were trials depicting human faces easier? The simplest answer is that the human stimuli that were selected at random had features that were simply more distinctive. Without the ability to ask subjects if a face is distinctive, there is no way to rule this out. It could also be true that the human faces were easier to match because they were higher in contrast than the chimpanzee or monkey faces, largely as a result of the background information. Another possibility is that the subjects have had more practice with isolated human features.

The logic here is straightforward; it would have been easier to respond accurately to this task if subjects were able to use features to diagnose individual identity. Now consider the subjects' previous experience with chimpanzee, monkey, and human faces. Both groups of subjects were raised and cared for by humans with plenty of contact with conspecifics. Their environment, therefore, increased their experience with the faces of conspecifics and human faces. Given that both groups combined have more experience with human faces than chimpanzee or monkey faces, experience alone might have accounted for the human face advantage if not for the null interaction between stimulus species and subject species. Instead, perhaps we should consider the kind of experience each subject has had with human faces. Human caretakers are required to wear personal protective equipment, including a mask that covers their

mouth and nose, when in close proximity to nonhuman primates. It seems reasonable to argue, therefore, that the subjects in this study not only had more experience with human faces, but potentially more practice using features to diagnose human identity.

Importantly, congruency did not interact with subject species providing empirical support for the notion that both chimpanzees and monkeys prefer to match global layout over local features. To date, researchers interested in testing general global-to-local processes have reported a difference between chimpanzees and rhesus monkeys. Previously, it has been concluded that only chimpanzees are consistently subject to interference from global shape when asked to analyze local details (Fagot and Tomonaga 1999; Hopkins and Washburn 2002) not monkeys (De Lillo et al 2005; Deruelle and Fagot 1997; Fagot and Deruelle 1997; Hopkins and Washburn 2002) and yet, when tested with faces, our monkeys, like our chimpanzees, tended to match global configuration over local features. This observation could be taken as further evidence that faces represent a distinctive high-level category of objects for which features are bound tightly together into a single unit of analysis (see McKone et al 2007).

Turning to the new configuration trials, we also found evidence that, while the subjects had a general tendency to match global configuration over local details, when they were asked to discriminate between two comparison stimuli with the same global configuration, it was harder to access local details when subjects had been trained with whole faces compared to scrambled faces.

Previous attempts to determine whether face processing is special in nonhuman primates have involved investigations of the face inversion effect, a replicable marker of holistic face processing in the human literature (Yin 1969). While numerous studies have demonstrated a face-inversion effect in nonhuman apes (Parr et al 1998; Parr and Heintz 2006; Tomonaga 1999, 2007) and monkeys (Dahl et al 2009; Neiworth et al 2007; Overman and Doty 1982; Tomonaga 1994; Vermeire and Hamilton 1998), some studies have failed to show that the inversion effect is larger for faces than for other object categories (Bruce 1982; Gothard et al 2004; Parr et al 1999; Weiss et al 2001), and others have suggested that face processing in nonhuman primates is not orientation-specific (Phelps and Roberts 1994; Wright and Roberts 1996). To further complicate matters, these studies have differed radically in task format, visual stimuli, and outcome measurements. For example, some researchers have drawn conclusions based on performance in trained, operant tasks (Bruce 1982; Parr et al 1998, 1999; Parr and Heintz 2006; Phelps and Roberts 1994; Tomonaga 1999, 2007) and others on changes in involuntary eye movements in habituation paradigms (Dahl et al 2009; Gothard et al 2004, 2009; Neiworth et al 2007).

In this study, we tracked holistic processing in a face discrimination task across two representatives of the primate order having used precisely the same method to test both species. We found that both species had more trouble generalizing from whole faces to a new configuration than from a learned scrambled configuration to new configuration. These data converge with the findings of previous studies to support the face-specific hypothesis by suggesting that both chimpanzees (Parr et al 2006) and monkeys (Dahl et al 2007; Taubert and Parr 2009) build holistic representations of faces but not other visually matched objects, such as scrambled faces. However, a stronger test of face specificity would need to consider the difference in vertical symmetry between whole faces and scrambled faces. If bilateral symmetry facilitates perceptual integration, then this would account for the current result and would predict the same result for any class of symmetrical objects and, thus, key questions remain with respect to cognitive specialization.

Performance in the new configuration trials was not dependent on long-term familiarity with the stimuli. Nonetheless, we would argue that the three-way interaction in the congruency trial was a symptom of visual experience. This result indicates that

chimpanzees experienced more interference in the chimpanzee-face condition than when matching human or monkey faces and, while the monkeys also experienced more interference in the conspecific condition, there were no significant differences across changes in the stimulus species (see figure 2b).

Infant humans (Pascalis et al 2002) and sensory deprived Japanese monkeys (Sugita 2008) have an initially broad ability to discriminate the faces of any species that narrows with visual experience. Perceptual narrowing for face discrimination explains why mature adults (Dahl et al 2009; Dufour et al 2006; Nelson 2003), chimpanzees (Parr et al 1998; Martin-Malivel and Okada 2007), and monkeys (Dahl et al 2009; Dufour et al 2006; Gothard et al 2009; Pascalis and Bachevalier 1998) have each demonstrated expert discrimination for faces of conspecifics but not for the faces of a species that has not been seen before. More recently, however, a number of studies have found the markers of expert face discrimination for unfamiliar species when testing rhesus monkeys (Parr et al 1999, 2008; Taubert and Parr 2009). For example when Parr et al (2008) tested rhesus monkeys with the faces of monkeys (conspecifics), humans, and chimpanzees (together with non-face objects) using the same match-to-sample that Parr et al used to test chimpanzees in 2000, they found holistic processing operated on any face, regardless of a subject's previous experience. In other relevant research, Taubert and Parr (2009) reported a composite face effect when they tested rhesus monkeys with chimpanzee faces. They inferred that holistic processing was operating on a category of unfamiliar faces; however a caveat to this study was the absence of a conspecific condition. In a more recent study that directly compared chimpanzees and rhesus monkey performance, familiarity with the stimulus set was found to change the perceptual strategy used by chimpanzees for face discrimination whereas the strategy used by rhesus monkeys appeared more stable (Taubert and Parr 2011). These studies, and others like them (for example Gothard et al 2009; Parr and Taubert 2011) have implied that rhesus monkeys are not as finely tuned to the morphology of their own species as chimpanzees. This difference is also clear in the present data implying that, for chimpanzees, global interference increases with familiarity but that, nonetheless, there is a clear bias towards global form.

Why would face discrimination in chimpanzees be more sensitive to experience than face discrimination in monkeys? One thing to consider is that chimpanzees, like humans, form social groups high on fission–fusion dynamics (Marlow 2005; Rodseth et al 1991). The term "fission–fusion" in this context refers to a society where group size regularly fluctuates by means of the joining and separating of smaller subgroups and individuals. Rhesus monkeys, in contrast, live in large multi-male, multi-female groups with a strict linear dominance hierarchy. Thus, although both chimpanzees and rhesus monkeys both live in large social groups, the groups formed by rhesus monkeys are more stable in the sense that group membership represents a life long commitment. It has been argued that fission–fusion societies are more sophisticated because the number of long-term relationships is not limited to group size and that this level of social complexity has driven changes in cognitive mechanisms (Amici et al 2008; Barrett et al 2003; Dunbar 1998). Perhaps, by moving between multiple social groups throughout life, chimpanzees are confronted with many more faces than rhesus monkeys and the high cost of processing a face limits the capacity of the face-processing system. Given the high probability that we will never again interact with the average stranger that we pass on the street, we restrict face processing for personally familiar faces and are more likely to use distinctive characteristics (such as skin color) to categorize unfamiliar faces. In sum, from this socioecological perspective, the chimpanzees were more tuned to conspecific morphology than monkeys because they were either born with a different face processing system, one more calibrated with the visual environment than the system inherited by monkeys, or their lifetime experience with faces was sufficiently

different from what the monkeys experienced that the system developed a greater sensitivity to own-species faces.

Another plausible explanation why monkeys have a global approach towards all faces is gaze avoidance. Monkeys perceive direct gaze as a threat and thus might avoid staring at faces, which would in turn limit the amount of fine detail that can be extracted from a face (Hinde and Rowell 1962). This could be determined by correlating eye movements with sensitivity to variance among faces. Whatever the reason, understanding why monkeys have the same cognitive approach to any face (while we and our closest living relative, the chimpanzee, are biased towards familiar faces) holds significant implications, not only for evolutionary psychology, but also for studies of human cognitive development.

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