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The organization of conspecific face space in nonhuman primates

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Humans and chimpanzees demonstrate numerous cognitive specializations for processing faces, but comparative studies with monkeys suggest that these may be the result of recent evolutionary adaptations. The present study utilized the novel approach of face space, a powerful theoretical framework used to understand the representation of face identity in humans, to further explore species differences in face processing. According to the theory, faces are represented by vectors in a multidimensional space, the centre of which is defined by an average face. Each dimension codes features important for describing a face's identity, and vector length codes the feature's distinctiveness. Chimpanzees and rhesus monkeys discriminated male and female conspecifics' faces, rated by humans for their distinctiveness, using a computerized task. Multidimensional scaling analyses showed that the organization of face space was similar between humans and chimpanzees. Distinctive faces had the longest vectors and were the easiest for chimpanzees to discriminate. In contrast, distinctiveness did not correlate with the performance of rhesus monkeys. The feature dimensions for each species' face space were visualized and described using morphing techniques. These results confirm species differences in the perceptual representation of conspecific faces, which are discussed within an evolutionary framework.

Keywords: Face space; Multidimensional scaling; Face identity; Rhesus monkey; Chimpanzee; Species differences.

Face recognition is a complex problem because all faces contain the same features—for example, eyes, nose, and mouth, arranged in the same general configuration (first-order configuration), yet our ability to discriminate between faces and recognize a face's identity appears effortless

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(Maurer, Le Grand, & Mondloch, 2002). One of the most popular and well-established explanations for this complex skill is that over many years humans develop an expertise with faces that enables the rapid and accurate detection of subtle changes in the size and spacing of facial features (second-order configuration), which are then integrated into a single perceptual representation—for example, identity—via holistic processing (Rhodes, Brake, & Atkinson, 1993; Rossion, 2008; Tanaka & Farah, 1993).

There has been considerable debate over the past 10 years as to whether these abilities reflect unique human specializations, or whether other nonhuman primates also represent face identity in similar ways. In the majority of studies conducted, researchers report similarities in the face-processing skills of chimpanzees and humans (Martin-Malivel & Okada, 2007; Parr, 2011b; Parr, Heintz, & Akamagwuna, 2006; Parr & Taubert, 2011; Parr, Winslow, Hopkins, & de Waal, 2000; Tomonaga, 1999, 2007; see Parr, 2011a, for a review of this literature). However, the literature is much less consistent with regard to similarities in the face-processing skills of monkeys compared to humans, where some recent studies have reported finding similarities (Adachi, Chou, & Hampton, 2009; Dahl, Logothetis, & Hoffman, 2007; Dahl, Wallraven, Bulthoff, & Logothetis, 2009; Gothard, Brooks, & Peterson, 2009; Gothard, Erickson, & Amaral, 2004; Pokorny & de Waal, 2009), while others have reported species differences (Bruce, 1982; Parr, 2011b; Parr & Taubert, 2011; Parr, Dove, & Hopkins; Parr, Heintz, & Pradhan, 2008; Parr, Winslow, & Hopkins, 1999; Parron & Fagot, 2008). These differences could be the result of differences in testing methodologies, selective looking versus operant testing paradigms, or they could reflect genuine species differences in face perception (see Parr, 2011a). Moreover, the approach of most studies has been to manipulate or mask some aspect of the face stimuli—for example, orientation, feature spacing, contrast, and so on, and then measure the effect on subjects' behaviour or performance. This approach is somewhat limited as faces contain many sources of information, and manipulating one source does not preclude subjects utilizing another. Moreover, the approach lacks a unifying theoretical focus and cannot be used to make predictions about the representation of face identity across species. Therefore, to provide a better understanding of the evolution of face-processing skills in primates, the present study used a face space framework to compare the representation of face identity in chimpanzees and rhesus monkeys.

Face space is a powerful theoretical framework for understanding the representation of face identity in humans and has been used to explain a variety of phenomena related to face processing, including distinctiveness and caricature effects, the face inversion effect, and other-race effects (Bruce, 1982; Byatt & Rhodes, 2004; Rhodes, Brennan, & Carey, 1987; Valentine, 1991; Valentine & Endo, 1992). According to the face space framework, faces are encoded as vectors in a multidimensional space (Figure 1). Each dimension reflects both physical and psychological attributes important for encoding a face's identity—for example, big nose, wide face, female, attractive, and so on. Experience may shape the sheer number of

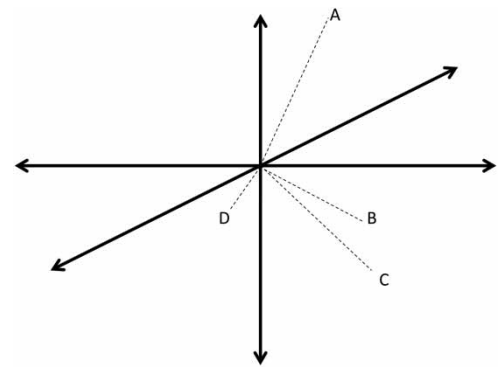

Figure 1. *A hypothetical illustration of a three-dimensional face space (Valentine, 1991). The origin of face space represents the central tendency of each feature dimension and is densely populated with faces of typical appearance. Each dashed line represents an identity vector that codes a unique face identity (A–D). Long vectors (e.g., A) indicate individuals of distinctive appearance in that their features are far from average, while short vectors (e.g., D) reflect typical individuals in that their features are more similar to the average.*

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dimensions present in face space, with a small number occurring for familiar faces in infancy and expanding as one's experience with faces grows throughout adulthood (Johnston & Ellis, 1995; Nishimura, Maurer, & Gao, 2009; Pedelty, Levine, & Shevell, 1985). Although the number and form of dimensions are unspecified, the location of each face in the multidimensional space encodes its unique combination of features. The origin (centre) of face space represents the central tendency of these dimensions, so faces located close to the origin are average, of typical appearance, while faces located farthest from the origin are distinctive (Valentine, 1991). In a familiar environment of own-race faces, typical faces represent the most frequently encountered faces making the origin of face space the most densely populated region (however, see Burton & Vokey, 1998). Because of this, discriminating between typical faces can be difficult, producing many false positives, while distinctive faces lie in sparsely populated regions, making them easier to discriminate.

The perceptual dimensions of face space can be visualized using multidimensional scaling analyses (MDS), a statistical technique that provides a graphical representation of the relative distances between stimuli based on their perceived dissimilarities. Based on the location of faces in the MDS plot, researchers can begin to interpret what features best characterize the perceptual dimensions of face space. The number of meaningful dimensions is typically identified from a scree plot, which shows the cumulative variance accounted for by each subsequent dimension. However, the interpretation of a multidimensional space is conceptually challenging, so studies of face space constrain the MDS solution to two or three dimensions. Using these techniques, several studies have explored the physical and psychological dimensions of human face space. Johnston and colleagues (Johnston, Milne, Williams, & Hosie, 1997), for example, examined the effect of distinctiveness on similarity judgements for male faces. Human participants rated all pairwise comparisons of 36 typical and distinctive faces on a 7-point scale. The similarity ratings were then subject to MDS analysis (2–6 solutions), and the distance from each face to the origin of face space was calculated (e.g., vector length) and correlated with the distinctiveness ratings. For all solutions, the vector length from the origin of face space was shorter for the 18 faces rated as most typical than for the 18 distinctive faces, supporting the basic architecture of face space (Valentine, 1991).

Lee and colleagues (Lee, Byatt, & Rhodes, 2000) created several categories of facial stimuli: the original veridical face and a set of their caricatures (faces in which distinctive features have been exaggerated), anticaricatures (faces in which distinctive features have been minimized), and the population average. Similar to Johnston and colleagues (Johnston, Milne, et al., 1997), they used MDS to plot the perceived dissimilarity between these images based on subjects' ratings. Their results confirmed that the highest exemplar density was near the origin and that the caricatures were located in more sparsely populated regions farthest from the both the average face and the origin of the face space. Thus, the caricatures were seen as being most distinctive and were located in the outermost regions of face space. Using a morphing technique, Busey (1998) also confirmed the utility of the face space model to understand the psychological representation of faces. They created a set of faces morphed between two identities, rated their typicality, and then examined the location of these morphs in an MDS plot of face space. As predicted by the face space model, the morphed faces were located between the two original identities, closest to the origin of face space, and the morphs were rated as more typical in appearance than either identity. This suggests that morphing functioned to reduce the distinctiveness of each face.

The face space model has also been used to examine the representation of age and gender in adults (Johnston, Kanazawa, Kato, & Oda, 1997), other-race effects (Byatt & Rhodes, 2004; Papesh & Goldinger, 2010), and developmental changes in face processing between infants and children. As young as 6 years, for example, children classify caricatures as being more distinctive than anticaricatures, and these effects are stronger after 8 years of age (Chang, Levine, & Benson, 2002). The

MDS technique has also shown that young children (under 10 years) appear to use fewer dimensions to differentiate faces than do older children and adults (Johnston & Ellis, 1995; Nishimura et al., 2009; Pedelty et al., 1985). These data suggest that face space is not a fixed construct but undergoes experiential changes throughout development in a manner similar to other experience-dependent changes in face perception, including perceptual narrowing and other-race effects (Pascalis, de Haan, & Nelson, 2002; Scott & Monesson, 2009; Slater et al., 2010). Under some conditions, the amount of time needed to form an average/prototype can be very short (Panis, Wagemans, & Op de Beeck, 2011). The importance of experience has been validated by autoassociation network models trained to discriminate either Caucasian or Asian faces (same race) and then tested for recognition among the untrained (other-race) faces. The distribution of these faces according to the variance accounted for by principal component analysis (PCA) modelling confirmed greater stimulus density and more difficult race categorizations for the untrained (other-race) faces than for the trained (same-race faces; Caldara & Abdi, 2006).

These results confirm that face space is an extremely influential model for understanding the representation of face identity in adults (Johnston, Milne, et al., 1997; Valentine, 1991), infants and children (Chang et al., 2002; Humphreys & Johnson, 2007; Jeffery et al., 2010; Johnston & Ellis, 1995; Pedelty et al., 1985), and clinical populations (Nishimura, Doyle, Humphreys, & Behrmann, 2010; Pellicano, Jeffery, Burr, & Rhodes, 2007). Although statistical approaches, such as MDS and other data reduction techniques, have been useful in visualizing the features important for the recognition of faces and facial expressions in monkeys (Kanazawa, 1996; Leopold, Bondar, & Geiese, 2006; Young & Yamane, 1992) and chimpanzees (Parr, Waller, et al., 2008), the results of these studies are often only interpreted subjectively without any strong theoretical context. When used together, however, the face space model is able to generate specific predictions about the perceptual representation of face identity, enabling cross-species comparisons that can be interpreted within a single theoretical framework. This approach provides a more objective basis for identifying and evaluating previously reported species differences in face identity processing in nonhuman primates (see Parr, 2011a, for a review). Therefore, it was the goal of this experiment to utilize a face space framework to compare similarities and differences in the

Figure 2. *An illustration of the matching-to-sample (MTS) paradigm used for chimpanzees. Subjects first contact the sample image (left panel) with the joystick-controlled cursor (shown by a cross). Then they select one of two comparison images (right panel), the correct image being identical to the sample face (lower right). This example shows female chimpanzee composites. The task was identical for the rhesus monkeys, only they selected images on a touchscreen. To view a colour version of this figure, please see the online issue of the Journal.*

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perceptual representation of face identity in two species of nonhuman primates: chimpanzees and rhesus monkeys. A subsequent goal was to interpret the distribution of faces in the MDS plot to identify what physical features were most important for discriminating face identity.

Using a simple discrimination task, both chimpanzees and rhesus monkeys were required to match every combination of 20 conspecific faces (380 pairs). This performance (% correct) is analogous to the use of similarity ratings between pairs of photographs in human studies. Humans who were experts with chimpanzees and rhesus monkeys were recruited using a web-based survey to provide the distinctiveness ratings for the face stimuli using a 5-point scale. The face space model predicts that the features important for the representation of face identity will be related to a faces' distinctiveness such that faces rated by human experts as most typical will cluster towards the origin of face space and be discriminated poorly, while the faces rated as distinctive will occupy peripheral locations and be easier to discriminate. Based on previous studies, we expect to find similarities in the basic organization of face space between chimpanzees and humans; however, monkey face space is not expected to be anchored by an average face, and discrimination performance is not expected to be related to a face's distinctiveness.

Method

Stimuli

The face stimuli used in both of these experiments consisted of composites made by averaging together 10 different photographs of each stimulus individual's face (Benson & Perrett, 1993). Previous studies in humans have demonstrated that composite images maximize the information diagnostic of individual identity by minimizing the visual information that is specific to the photograph, such as background, hue, lighting, and contrast. This information is not relevant for the recognition of individual identity and can even interfere because the variance in pictorial cues across photographs tends to outweigh the variance across faces. This can create a situation in which photographs of different individuals appear more similar to one another than photographs of the same individual (Burton, Jenkins, Hancock, & White, 2005; Jenkins & Burton, 2011). The composite images produce robust recognition advantages with small numbers of images. Error rates in recognizing a person's identity from a composite image, for example, become negligible after combining only 10–12 images (Burton et al., 2005). This stability also appears to be independent of which specific exemplar photographs are used, such that two composite images showing the same individual, but made using different sets of photographs, will appear highly consistent to one another. Finally, advantages in recognizing a person's identity from composite image compared to a single image remains robust even when the composite image is contaminated by the inclusion of an erroneous photograph depicting a different individual (for a review, see Jenkins & Burton, 2011).

To create the face composite stimuli, photographs were acquired from male and female chimpanzees living at the MD Anderson Cancer Center in Bastrop, TX, and rhesus monkeys at the Yerkes National Primate Research Center field station, Lawrenceville, GA. Photographs were taken outside during overcast weather conditions or when subjects were in the shade so as to minimize the influence of shadows or differences in lighting that might bias the quality of the composite. Important for the creation of the individual composites was that each photograph be taken at a different "sitting" and not all from the same time point when the subject remained in the same position. This helped to ensure that the visual information averaged in each photograph was not biased by the overrepresentation of a particular background or lighting condition, and that each composite averaged a reasonable estimate of the range of variance present in different photographs (Burton et al., 2005). Only photographs that depicted relatively full-frontal orientations were used. Before creating the composites, each photograph was standardized by rotating it in-plane so that the interpupil distance was horizontally aligned and then cropping closely around the head. Each photograph was then

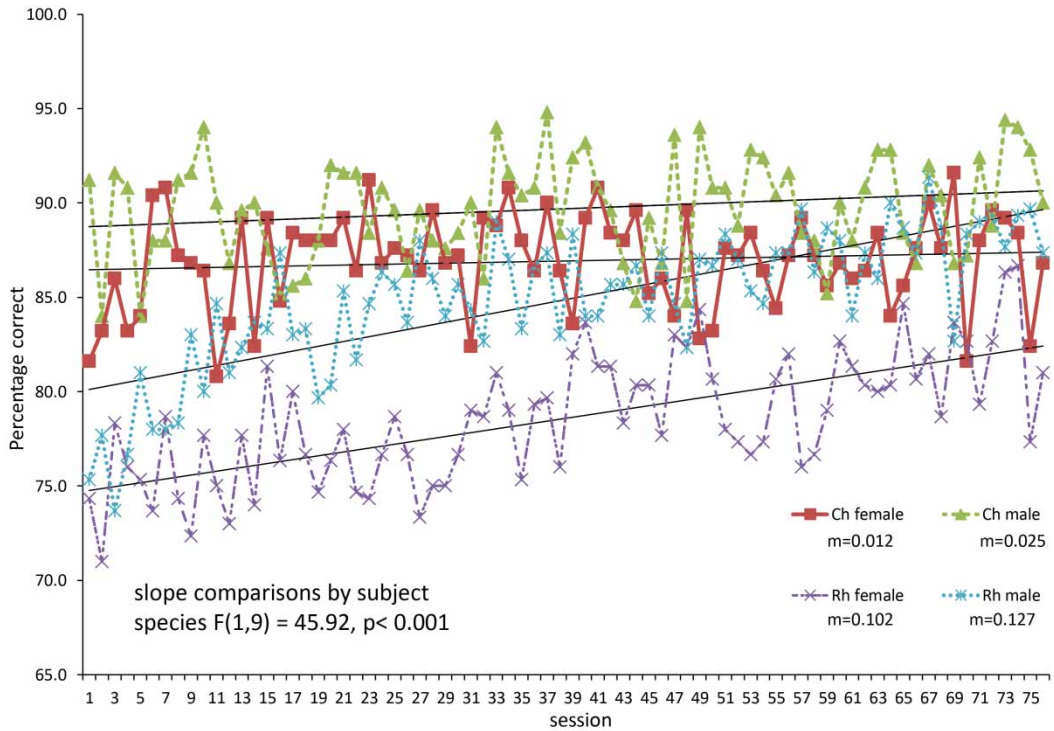

Figure 3. *The mean performance of chimpanzees (Ch) and rhesus monkeys (Rh) over the seventy-six 50-trial sessions (*m = *slope values for the group means). To view a colour version of this figure, please see the online issue of the Journal.*

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resized to 700 pixels in height. Using Psychomorph software (Tiddeman, Burt, & Perrett, 2001), 188 points were then positioned on each chimpanzee face to delineate specific facial landmarks, and 106 points were used to delineate the features of the monkey faces. This difference was due to a greater number of morphological features in the eye region —for example, distinctive wrinkles under the eyes, across the muzzle, and defining the ear region—of chimpanzees than of rhesus monkeys (see SOM_Figure 3). Composite images were created by calculating the mean shape for each set of images and each image warped to the average shape. The images were then superimposed to create an image with the average shape and colour of the constituents (Rowland & Perrett, 1995; Tiddeman et al., 2001). The averages were rendered with a texture algorithm (wavelet) to minimize blurring that can occur as a result of the averaging process (Tiddeman et al., 2001).

There were 80 total face composites used in this study: 40 chimpanzees and 40 rhesus monkeys (20 males and 20 females). Of the 20 face composites for each species/gender, 19 depicted specific individuals—for example, John, Mary, and so on. The final composite face was a population average created by averaging together the faces of 20 different individuals from each species and gender category. So, four population average faces were created, one for each species/gender stimulus category. All of the stimulus individuals were unfamiliar to the subjects of this study.

Subjects

Five chimpanzees (3 males and 2 females) ranging in age from 17 to 23 years participated voluntarily in these studies. The chimpanzees were raised by humans in peer groups at the Yerkes Primate Center until 4 years of age when they joined established social groups. All chimpanzees were socially

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housed and were tested twice daily in their home cage using a computerized-joystick testing protocol (see Parr et al., 2000). All chimpanzees had extensive experience performing computerized tasks of face recognition using matching-to-sample (MTS) prior to this study (reviewed by Parr, 2011a).

Six rhesus monkeys (2 males and 4 females), approximately 10 years of age, participated in these studies. The monkeys were raised by their mothers in large social groups at the Yerkes Primate Center field station until 4 years of age when they were moved to the main centre to participate in experiments of face recognition. The monkeys were pair housed (same gender) in the same colony room and were tested twice daily in their home cage using a computerized-touchscreen testing protocol (see Parr, Heintz, & Pradhan, 2008). All monkeys had extensive experience performing computerized tasks of face recognition using MTS prior to this study (reviewed by Parr, 2011a).

Prior to this experiment, neither the chimpanzee nor rhesus monkey subjects had ever been presented with composite face images. All procedures used in these studies were approved by the Institutional Animal Care and Use Committee of Emory University.

Procedure

Cognitive testing using matching-to-sample. All animal subjects were tested using a computerized MTS task. Chimpanzees selected images using a joystick-controlled cursor while monkeys used a touchscreen interface. According to the MTS procedure, animal subjects were first shown a single face, referred to as the sample, on the computer monitor. This was presented centrally against one of the four sides of the computer monitor. After orienting to this image by contacting it with the joystick-controlled cursor (procedure for the chimpanzees) or touching it three times in rapid succession on the touchscreen monitor (procedure for the monkeys), two additional faces were presented simultaneously on the screen located equidistant from the sample on the opposite side of the monitor. One of these faces (target) was identical to the sample, while the other (foil) showed the face of a different conspecific (see Figure 2). A correct response to the target image was reinforced with a small food item and was followed by an intertrial interval (ITI) of 2 s, while an incorrect response to the foil was followed by an ITI of 5 s and no food reward. The next trial was then presented.

For the purposes of this study, the animal subjects only discriminated conspecifics' faces, and because face gender may be represented differently in face space, having distinct norms (Johnston, Kanazawa, et al., 1997; Little, DeBruine, Jones, & Waitt, 2008), male and female faces were tested separately. For both species, photographs of the female faces were acquired more quickly than those of the male faces, so female faces were tested first, followed by the male faces. The task was organized so that the matching pair of faces (sample plus target) showed identical composites, and these were paired with every other composite as the foil. Thus, 380 unique trials were created (20×19) for each species/gender category, representing every dyadic combination of faces within each category. Each face dyad, representing one trial, was repeated 10 times, totalling 3,800 trials. Before testing began, the 3,800 trials were randomly divided into seventy-six 50-trial blocks, and the animal subjects received two 50-trial testing blocks per day until all 76 blocks had been completed. Each animal subject was tested using a different, random block order. The discrimination performance data (% correct) were then subject to MDS analysis.

Facial distinctiveness ratings by human experts. Using a web-based survey, distinctiveness ratings for the 20 face composites in each of the four species/gender categories were gathered from humans who had experience working directly with chimpanzees and rhesus monkeys. The human experts were recruited by e-mail invitation to rate the composite faces using a 5-point rating scale (1 = very typical, 2 = somewhat typical, 3 = interesting, 4 = unusual, 5 = highly distinctive). They were additionally asked to list their experience working with each species (<1 year, 1–5 years, 6–10 years, and >11 years), the approximate number of individuals they considered themselves familiar with (<5, 6–20, 21–50, and >51

Table 1. *Information pertinent to the experience of human chimpanzee and rhesus monkey experts who rated the face composites based on their distinctiveness*

		Rating		*Years of experience*				*No individuals*			
Face	*No. raters*	*Mean (+SEM)*	*Min/max*	*<1*	*1–5*	*6–10*	*>11*	*<5*	*6–20*	*21–50*	*>51*
C Female	42	2.55 (0.16)	1.40/4.07	2	20	12	8	0	10	12	20
C Male	28	2.75 (0.21)	1.46/4.46	1	12	7	8	2	8	8	10
R Female	27	2.62 (0.14)	1.19/3.89	0	9	8	10	0	8	4	15
R Male	40[a]	2.58 (0.13)	1.43/3.50	3	10	13	14	0	8	5	26

Note: C = chimpanzee; R = rhesus monkey. No. individuals = number of individuals that respondents were familiar with.
[a]One person responding to the rhesus male survey did not report how many individuals they were familiar with.

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individuals), and the degree to which the face was an important visual feature for identifying individuals (1 = not at all, 2 = face is important with other features, 3 = the face is primarily how individuals are recognized, 4 = will not make positive identification without seeing the face). These data were not analysed but were used to validate the expertise of the human raters (see Table 1). Because the survey responses were anonymous and were acquired at different times for the four stimulus categories, they were not necessarily rated by the same individuals. The surveys for each gender/species were available online for a 3-month period, after which the rating data were downloaded and saved for analysis.

Data analysis

The animal subjects' performance discriminating each of the 20 male and female face composites was averaged across foil types. This produced an overall percentage correct for each face. Pearson's product moment correlations were then used to compare this overall performance with the human experts' mean distinctiveness ratings. We hypothesized that subjects' discrimination performance would correlate positively with the human experts' distinctiveness ratings, so that the best performance would occur for the most distinctive faces.

Next, the animal subjects' mean performance discriminating each of the 380 individual face dyads in each gender category was entered into a square asymmetrical matrix and was subjected to a multidimensional scaling analysis (MDS–Proxscal) using a Euclidean distance scaling model following the guidelines of Garson (http://faculty.chass.ncsu.edu/garson/PA765/index. htm). The MDS derives a distance measure between each pair of faces that reflects their perceived dissimilarity—the farther apart the faces lie, the greater their dissimilarity (Everitt & Dunn, 2001). This was initially performed using a 2–6-dimension solution to evaluate of the number of dimensions that best described the data sets. However, because the visual interpretation of MDS plots containing more than 2 dimensions can be challenging, the remainder of the analyses were constrained to a 2D solution. The derived stimulus configurations graphed in the 2D solution reflect the degree of perceptual dissimilarity among the faces, and this approach has been used in previous studies in humans to provide a graphical plot analogous to the perceptual dimensions of face space from which specific hypotheses can be drawn (Johnston, Kanazawa, et al., 1997; Johnston, Milne, et al., 1997; Nishimura et al., 2009; Valentine, 1991).

Using the 2D framework, we quantified *vector length*, the linear distance between each face from the origin (0:0) as a measure of its distinctiveness. The population average face was hypothesized to have the shortest vector, lying closest to the origin and representing the most typical face. Pearson's product moment correlations were used to evaluate the relationship between vector length and the mean distinctiveness ratings provided by the human experts. Significant positive correlations

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were expected between the humans' face distinctiveness ratings and vector length. The longer the vector, the more distinctive the face's rating. Moreover, if the average face represents the central tendency of the feature space, then it is expected to have the shortest vector, falling closest to the origin of face space.

Finally, to determine whether the origin of face space was the most densely populated region, we calculated the mean interstimulus distance as a proxy for *stimulus density*, where longer distances reflected lower density. Then, using the median split of the vector lengths, we divided the faces into two groups: those falling close to the origin of face space and those falling in the periphery. A univariate analysis of variance (ANOVA) was then used to compare whether the stimulus density for each composite face differed between these two regions.

Results

Distinctiveness ratings by human experts

Table 1 lists the mean (+*SEM*), minimum, and maximum distinctiveness ratings provided for both the male and female face composites by the human chimpanzee and rhesus monkey experts. It additionally lists the length of experience that the experts had working with those species and the approximate number of individuals with whom they had familiarity. Independent *t* tests were used to evaluate whether the humans' perception of chimpanzee and rhesus monkey face distinctiveness showed marked differences. No significant differences were found for the distinctiveness ratings between the male chimpanzee and the rhesus monkey faces, $t(38) = 0.70$, $p = .49$, or the between the female chimpanzee and the rhesus monkey faces, $t(38) = 0.32$, $p = .75$.

Chimpanzee subjects' performance data

Overall, chimpanzees discriminated the face composites well. Performance matching male conspecifics' faces (mean = 89.65%, *SEM* = 0.90, range 83.47% to 96.63%) was better than that matching the female conspecifics' faces (mean = 86.93%, *SEM* = 1.25, range 75.79% to 95.26%), but this did not reach significance, $F(1, 38) = 3.11$, $p = .086$. To determine whether performance changed over time, a slope value was derived from subjects' mean performance over each of the seventy-six 50-trial testing sessions (Figure 3). These slope values were very low (female = 0.012; male = 0.025), suggesting that there was no cumulative increase or decrease in performance over time, and they were not significantly different, $t(4) = 0.39$, $p = .72$.

Visualizing the perceptual dimensions of chimpanzee face space using MDS

Initially, a 2–6-dimension MDS (Proxscal) solution was derived for the male and female chimpanzee face composites based on 100 iterations of each matrix until the stress value could be improved by no more than 0.001 (SPSS 17.0). Four and three iterations met this criterion for female and male chimpanzee faces, respectively. The number of dimensions that best described the data was interpreted from the scree plots showing the normalized raw stress scores for each dimension. Four dimensions were optimal for both the female and male chimpanzee faces. The MDS analysis provides several measures of stress indicating how well the derived distances reflect the input data (Kruskal & Wish, 1978). Using a 4D solution, the Kruskal's stress formula 1, where 0 is the best and 1 is the worst fit, was .18 for the female chimpanzee faces and .19 for the male chimpanzee faces. The mean dispersion accounted for (e.g., goodness-of-fit) by the derived distances was .97 and .96 for the female and male chimpanzee faces, respectively. This indicates the proportion of variance explained by the derived distances. The MDS analysis was then constrained to a 2D solution to provide a graphical plot analogous to the perceptual dimensions of face space (described above). Figures 4 and 5 show the derived stimulus configurations for the female and male chimpanzee faces. Table 2 lists the mean performance of chimpanzees matching each of the 20 female and 20 male conspecific face composites (averaged across foil types), the mean typicality ratings for these stimuli made by the human experts, the vector length calculated from the 2D MDS plot, and the mean interstimulus distance (ISD), where large values reflect low stimulus density.

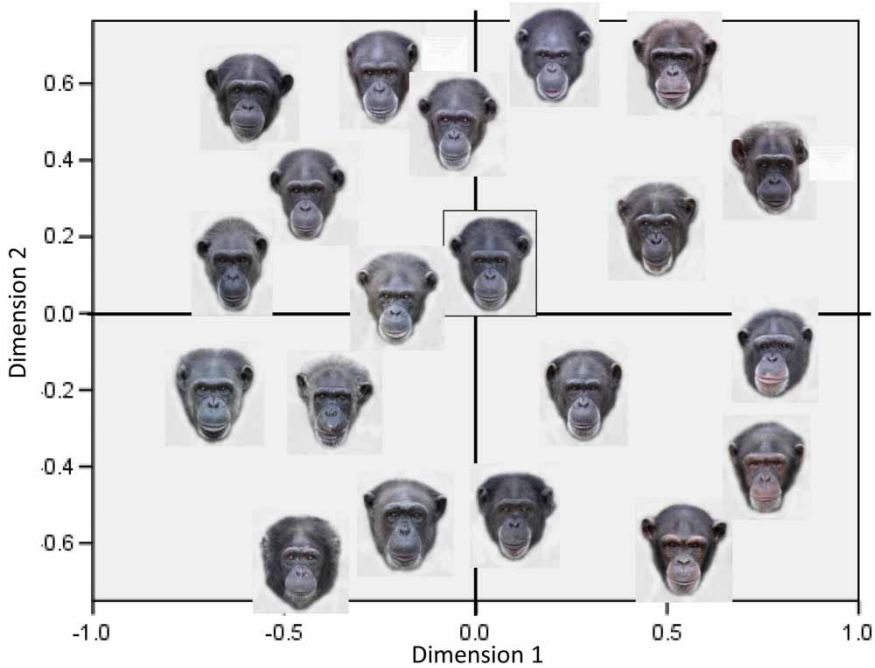

Figure 4. *The derived stimulus configuration for female chimpanzee faces based on a 2D multidimensional scaling (MDS) analysis of subjects' discrimination performance. The average face is outlined. To view a colour version of this figure, please see the online issue of the Journal.*

An analysis of the MDS plot shown in Figure 4 confirmed each of our hypotheses. The female chimpanzee population average face (outlined) had the shortest vector (0.10), falling closest to the origin of face space, was rated by the human chimpanzee experts to be the least distinctive face (1.40), was the most difficult face to discriminate based on the chimpanzees' overall performance (75.79% averaged across foil types), and had the shortest mean interstimulus distance (0.65), indicating that it was the most densely interconnected face in face space. Pearson product moment correlations confirmed significant positive correlations between human chimpanzee experts' distinctiveness ratings and vector length, $r = .55$, $p < .02$, and human chimpanzee experts' distinctiveness ratings and the chimpanzees' face discrimination performance, $r = .58$, $p < .01$. Faces rated as more distinctive had longer vectors and were discriminated better than typical faces.

The picture was similar for the male chimpanzee faces, but several differences were also observed. An analysis of the MDS plot shown in Figure 5 revealed that the shortest vector (0.24) and shortest mean interstimulus distance (0.69) were for Martin's face (see Table 2), followed by the male chimpanzee population average face (0.40 vector length vs. 0.71 ISD). The human chimpanzee experts rated the male chimpanzee population average face as "somewhat typical", but these ratings did not correlate significantly with the chimpanzees' discrimination performance, $r = .34$, $p < .14$. The chimpanzees' performance discriminating the population average male chimpanzee face was 85.25%, with only four other male faces having as low or lower performance. There was, however, a significant positive correlation between vector length and the human chimpanzee experts' distinctiveness ratings, $r = .48$, $p < .04$. Faces rated as more distinctive had longer vectors.

In order to address whether the centre of face space was the most densely populated region, the male and female chimpanzee faces were each divided into two groups using a median split of

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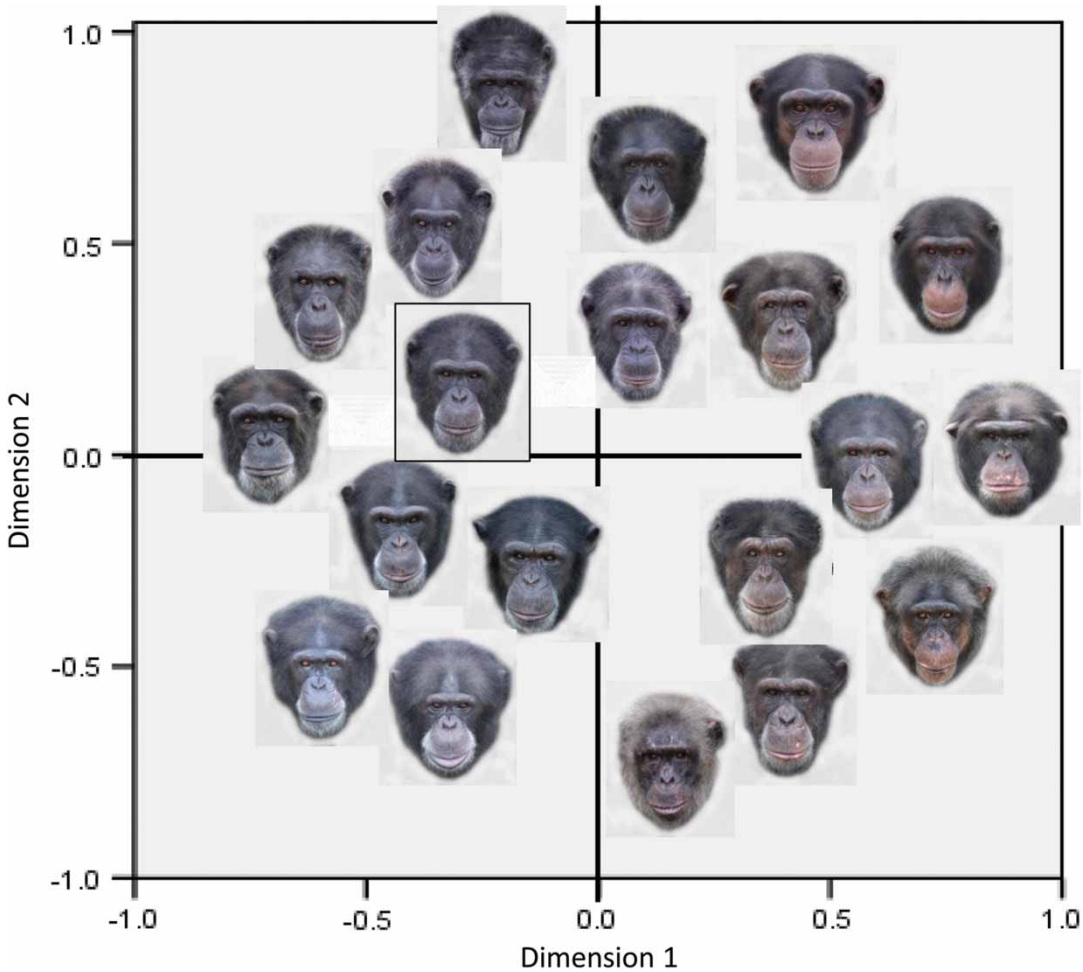

Figure 5. *The derived stimulus configuration for male chimpanzee faces based on a 2D multidimensional scaling (MDS) analysis of subjects' discrimination performance. The average face is outlined. To view a colour version of this figure, please see the online issue of the Journal.*

their vector lengths. Then, the mean interstimulus distance, as a proxy for stimulus density, was analysed for each group of faces using a one-way ANOVA where vector length (short vs. long) was the between-group factor. This revealed a significant difference in stimulus density for both the female, $F(1, 18) = 54.20$, $p < .001$, and the male chimpanzee faces, $F(1, 18) = 60.92$, $p < .001$. The chimpanzee faces located closer to the origin of face space (short vectors) were more densely clustered, having shorter interstimulus distances, than faces located far from the origin of face space (long vectors).

Rhesus monkey performance data

Overall, the rhesus monkeys discriminated the conspecific face composites well, but their performance was significantly greater for the male (mean = 84.67%, $SEM = 1.18$, range 73.86% to 91.32%) than for the female monkey faces (mean = 78.60%, $SEM = 1.57$, range 62.37% to 88.42%), $F(1, 38) = 9.53$, $p < .004$. To determine whether performance changed over time, a slope value was derived from the monkeys' performance over the 76 testing sessions (see Figure 3). These slope values were significant larger for the monkeys'

Table 2. *Mean distinctiveness ratings provided by human chimpanzee and rhesus monkey experts for male and female faces, mean performance by subjects discriminating each face, the vector length between each face and the origin of the MDS plot, and the mean interstimulus distance*

Females						*Males*					
	Rating						*Rating*				
Name	*Mean*	SEM	*Mean % correct*	*Vector length*	*Mean ISD*	*Name*	*Mean*	SEM	*Mean % correct*	*Vector length*	*Mean ISD*
Chimpanzees											
Average	1.40	0.16	75.79	0.10	0.65	Lyle	1.46	0.16	92.53	0.50	0.78
Jessie	1.45	0.19	82.11	0.27	0.66	Austin	1.54	0.16	84.53	0.45	0.75
Nina	1.71	0.17	85.47	0.68	0.89	Gage	1.71	0.19	96.63	0.90	1.01
Hodari	1.83	0.20	81.47	0.38	0.85	Oscar	1.75	0.14	91.26	0.81	0.97
Lulu	2.14	0.20	89.16	0.75	0.93	Alex	1.93	0.20	90.84	0.60	0.87
Sophie	2.14	0.20	79.26	0.35	0.76	Average	2.00	0.22	85.26	0.40	0.71
Sindee	2.17	0.26	93.26	0.91	1.02	Magic	2.29	0.21	84.00	0.46	0.84
Monique	2.31	0.22	85.58	0.23	0.72	Chester	2.29	0.25	85.26	0.51	0.78
Kaya	2.36	0.26	84.53	0.66	0.91	Martin	2.36	0.21	88.63	0.24	0.69
Muffin	2.45	0.22	83.26	0.54	0.78	Billy	2.50	0.26	85.79	0.45	0.74
Tasha	2.52	0.26	94.53	0.96	1.02	Kudzu	2.50	0.20	87.26	0.60	0.88
Tina	2.67	0.21	94.74	0.94	1.02	Keno	2.64	0.23	89.47	0.72	0.94
Tanya	2.64	0.23	86.63	0.50	0.79	Cesar	3.14	0.23	88.84	0.61	0.87
Angie	2.98	0.24	81.47	0.42	0.84	Huhni	3.18	0.26	92.53	0.83	0.98
Jane	3.00	0.26	86.74	0.56	0.85	Mahsho	3.43	0.31	83.47	0.48	0.76
Cheopi	3.02	0.27	91.37	0.85	0.99	Cordova	3.50	0.27	90.42	0.79	0.95
Melissa	3.17	0.28	92.11	0.79	0.95	Pecos	3.93	0.26	95.89	0.92	1.02
Pepper	3.26	0.31	84.53	0.54	0.78	Nowi	4.11	0.29	93.79	0.86	0.98
Nahja	3.67	0.26	91.26	0.91	1.02	Ehsto	4.36	0.24	92.53	0.76	0.95
Tuppence	4.07	0.24	95.26	0.86	0.99	Kalioni	4.46	0.23	94.00	0.84	0.99
Rhesus monkeys											
Average	1.19	0.11	81.93	0.78	0.96	m10	1.85	0.21	0.76	88.51	0.95
Tf9	1.85	0.20	83.16	0.89	0.99	mx131	3.18	0.33	0.79	89.65	0.97
Qz9	1.96	0.20	71.40	0.63	0.90	m181	1.75	0.21	0.81	87.81	1.00
Sc9	1.96	0.20	80.00	0.52	0.78	m239	2.43	0.24	0.67	91.23	0.89
Dc8	2.15	0.27	86.75	0.86	0.96	eb7	2.45	0.25	0.51	83.07	0.79
Tq3	2.26	0.26	74.12	0.21	0.68	ff72	2.43	0.24	0.72	86.40	0.93
Es10	2.48	0.24	62.37	0.27	0.69	fh21	1.65	0.18	0.17	73.86	0.66
Vk2	2.48	0.27	70.18	0.35	0.80	ga20	2.98	0.29	0.79	91.32	0.98
Yw3	2.48	0.28	85.88	0.93	1.02	gw3	3.50	0.25	0.53	79.39	0.80
Sz5	2.56	0.28	78.07	0.50	0.75	kl11	2.58	0.26	0.72	88.51	0.92
Ry8	2.63	0.26	73.60	0.45	0.82	ks5	2.45	0.26	0.30	79.65	0.70
Nm8	2.70	0.24	79.12	0.77	0.95	op10	2.30	0.25	0.75	88.77	0.95
Zj8	2.74	0.20	70.88	0.39	0.71	Average	1.43	0.22	0.57	82.54	0.83
Mg9	2.85	0.32	75.00	0.62	0.89	rv5	3.48	0.27	0.69	81.23	0.89
Yc3	3.04	0.31	85.09	0.88	0.99	sf6	2.70	0.24	0.53	80.79	0.79
Zq3	3.04	0.29	87.89	0.62	0.84	ts9	2.78	0.31	0.25	75.00	0.67
Eh5	3.15	0.25	84.04	0.65	0.91	ua6	2.43	0.25	0.35	80.61	0.71
Bd8	3.26	0.25	73.86	0.58	0.85	uj11	2.95	0.31	0.82	89.91	1.01
Pp8	3.67	0.32	80.26	0.72	0.94	yf10	3.08	0.26	0.80	87.11	0.98
Cf5	3.89	0.24	88.42	1.00	1.03	zy5	3.23	0.27	0.81	87.98	0.99

Note: Distinctiveness ratings: means + standard error of the mean (*SEM*). Larger values indicate greater distinctiveness. Performance: % correct. Face discrimination averaged across foil types. ISD = interstimulus distance, where large values reflect low density. MDS = multidimensional scaling.

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performance than for the chimpanzees' performance, $F(1, 19) = 45.92$, $p < .001$ (female = 0.102; male = 0.127), but a paired t test showed that there was no difference between the slope of performance by monkeys discriminating the female compared to male rhesus faces, $t(5) = 1.10$, $p = .32$.

Visualizing the perceptual dimensions of rhesus monkey face space using MDS

Similar to the chimpanzees' data, an initial MDS analysis was performed on the monkeys' performance data. This required 8 iterations for the female monkey faces and 5 for the male monkey faces. Four dimensions were also optimal in accounting for the greatest variability in the monkeys' performance discriminating conspecifics' faces. Using this 4-dimension solution, the Kruskal's stress formula 1 for the male and female rhesus monkey faces was .19. The mean dispersion accounted for (e.g., goodness-of-fit) by the derived distances was .96 and .97 for the female and male rhesus monkey faces, respectively. The MDS analysis was then constrained to two dimensions. Figures 6 and 7 show the derived stimulus configurations for the female and male rhesus monkey faces, respectively. Table 2 lists the mean performance of monkeys matching each of the 20 female and 20 male monkey face composites (averaged across foil types), the mean typicality ratings made by the human rhesus monkey experts, the vector length calculated from the 2D MDS plot, and the mean ISD.

The MDS plots shown in Figure 6 and 7 revealed that neither the male nor the female rhesus monkey population average face (outlined) was located close to the origin of face space. Interestingly, the human rhesus monkey experts rated the population average monkey faces (both male and female) as least distinctive, and these ratings were not significantly correlated with the monkeys' discrimination performance for either the female monkey face composites, $r = .17$, $p = .47$, or the male rhesus monkey face composites, $r = .11$, $p = .63$, or vector length (female: $r = .16$, $p = .51$; male: $r = .26$, $p = .27$). Overall, the population average rhesus monkey faces were not difficult for the monkeys to discriminate, 81.93% for the female average, which was the 8th best performance, and 82.54% for the male average, which was the 13th best performance (of the 20 composites in each gender category).

The same procedures as those used for the chimpanzee were applied to address whether the centre of face space was the most densely populated region for the monkey's face space. A univariate ANOVA using vector length (short vs. long) as the between-group factor revealed a significant difference in stimulus density for both the female, $F(1, 18) = 47.25$, $p < .001$, and the male rhesus monkey faces, $F(1, 18) = 47.36$, $p < .001$. The faces located closer to the origin of face space (short vectors) were more densely clustered, having lower interstimulus distances, than faces located far from the origin of face space (long vectors). The population average female monkey face fell in the distinctive group, while the population average male monkey face fell in the typical group, based on the median split of the vector lengths for all 20 faces in each category.

Interpreting the dimensions of face space

Interpreting the feature dimensions of face space can be challenging, even when the MDS plot is constrained to two dimensions. In some studies, researchers have been able to label the dimensions by noting the location of each stimulus face in the MDS plot and interpreting similarities and differences in their features (Parr, Waller, et al., 2008). Using similar methods, important features for human face recognition have included age, race, species, face width, and facial hair (Busey, 1998; Johnston, Kanazawa, et al., 1997; Little et al., 2008; Pedelty et al., 1985). In other studies, however, finding clear labels for each dimension has been more difficult, particularly if these involve a combination of features that cannot easily be verbalized or may be codependent on other cues, which can be a limitation when narrowing the MDS plot to show only two dimensions. In the present study, we used two approaches to interpret the perceptual dimensions of face space revealed by the MDS analyses above. First, we attempted to label the dimensions by visual

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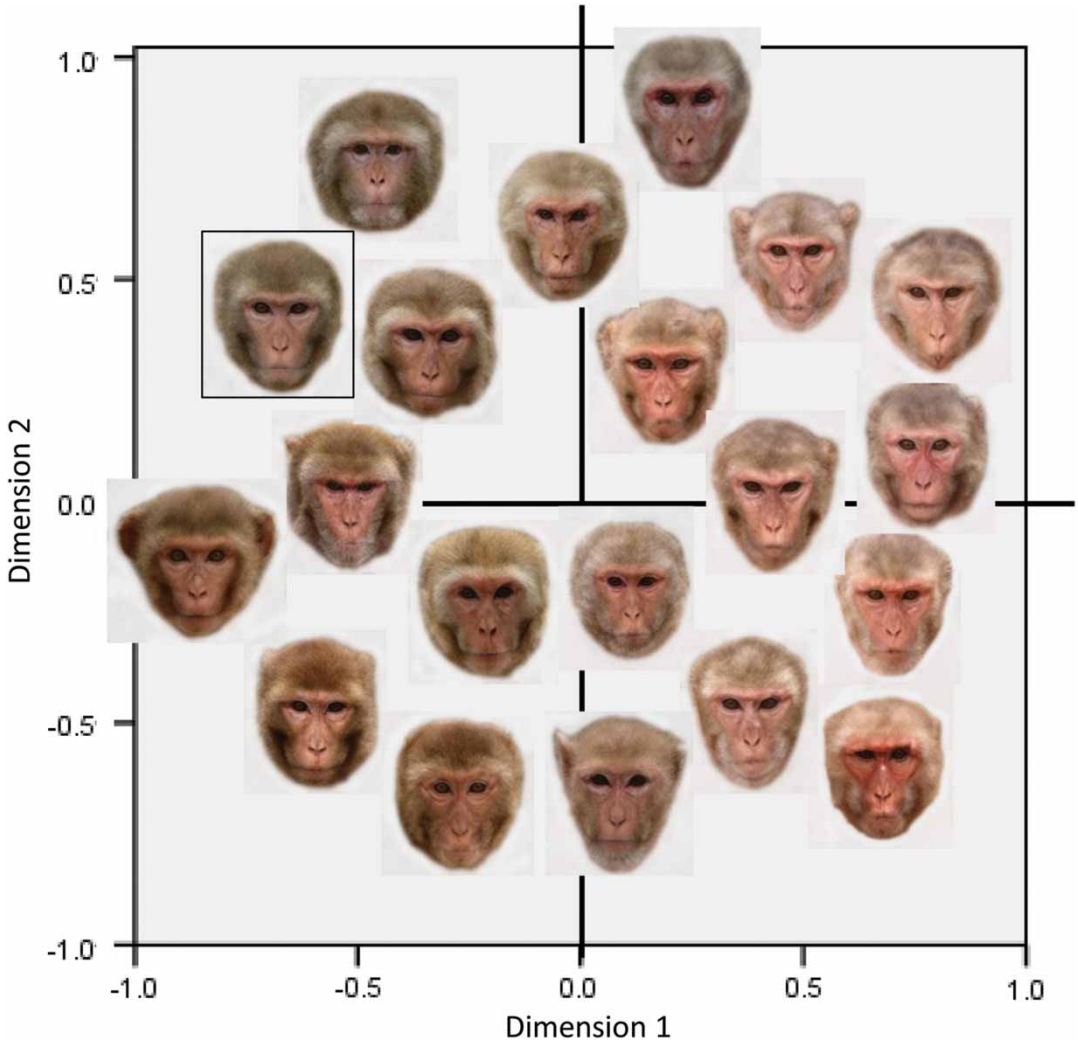

Figure 6. *The derived stimulus configuration for female rhesus monkey faces based on a 2D multidimensional scaling (MDS) analysis of subjects' discrimination performance. The average face is outlined. To view a colour version of this figure, please see the online issue of the Journal.*

inspecting the location of each face composite stimulus on the 2D MDS plots and interpreting similarities and differences in observable features (Parr, Waller, et al., 2008). For the female chimpanzee faces shown in Figure 4, this proved to be difficult. Four of the six individuals high on Dimension 1 (>.5) had faces or muzzles that were browner in coloration than those individuals at the low end of Dimension 1. So, Dimension 1 might be defined by facial coloration. A similar interpretation was plausible for the male chimpanzee faces (Figure 5). Several of the individuals located on the high end of Dimension 1 had browner muzzles and contrasting facial patterns compared to the individuals on the low end of Dimension 1. Dimension 2 could not be easily labelled for either the female or the male chimpanzee faces.

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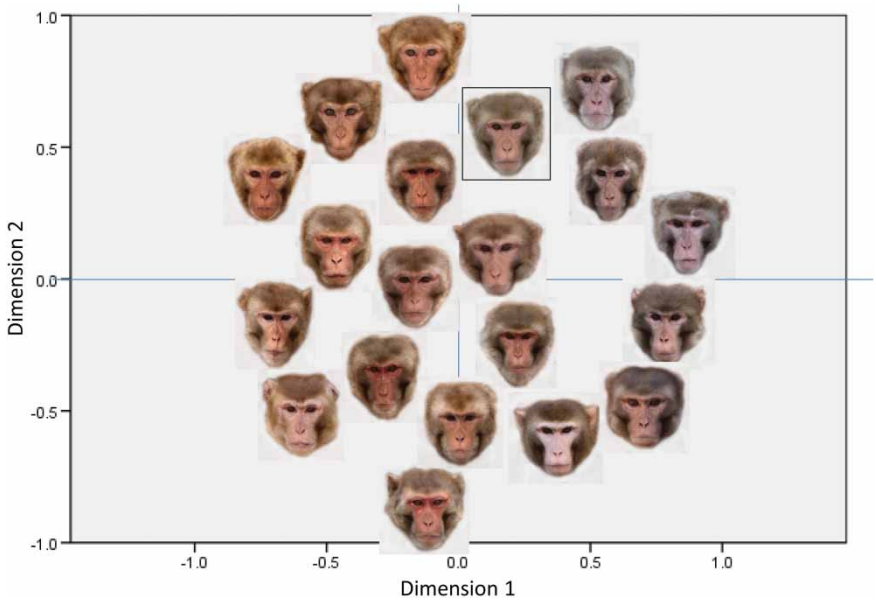

Figure 7. *The derived stimulus configuration for male rhesus monkey faces based on a 2D multidimensional scaling (MDS) analysis of subjects' discrimination performance. The average face is outlined. To view a colour version of this figure, please see the online issue of the Journal.*

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The same initial visualization approach was applied to the derived stimulus configuration plots for the rhesus monkey faces. This inspection showed that for both the female and male rhesus monkey faces, Dimension 1 had a clear and prominent colour/brightness component. For the female monkey faces shown in Figure 6, the individual faces located at the high end of Dimension 1 appeared brighter and had lighter hair colour than faces at the low end of Dimension 1. These individual faces appeared darker and had more reddish coloured hair. Additionally, Dimension 1 appeared to characterize something about face size and shape. Individuals at the high end of Dimension 1 had smaller, more triangular-shaped faces than the individuals at the low end of Dimension 1 whose faces appeared rounder and larger. For the male rhesus monkey faces shown in Figure 7, Dimension 1 also appeared to reflect the colour of the faces, with the faces at the high end of Dimension 1 appearing to have a more bluish, earthy tone whereas the faces at the low end of Dimension 1 had a more reddish tone. There was no clear interpretation for Dimension 2. A post hoc analysis of colour is provided in the next section below.

Nishimura and colleagues (2009) attempted to overcome the difficulties inherent in visually interpreting the MDS solutions by averaging together the individual faces located at the extremes of each dimension and then asking people to rate the observable features in these high/low dimension averages. This strategy has the advantage over visual inspection in that more than two dimensions may be evaluated from the stimulus coordinates produced by the optimal MDS solution—for example, we could evaluate all four dimensions from our analyses. Therefore, our second approach was to average the face composites located at the extreme endpoints of the 4D MDS solutions (based on their spatial coordinates), resulting in eight averages that represent the high and low values for each of the four feature dimensions. Psychomorph was used to symmetrize these faces and then transform each population average into their template space. The transformation was performed along a dynamic continuum that exaggerated the shape differences defined by each

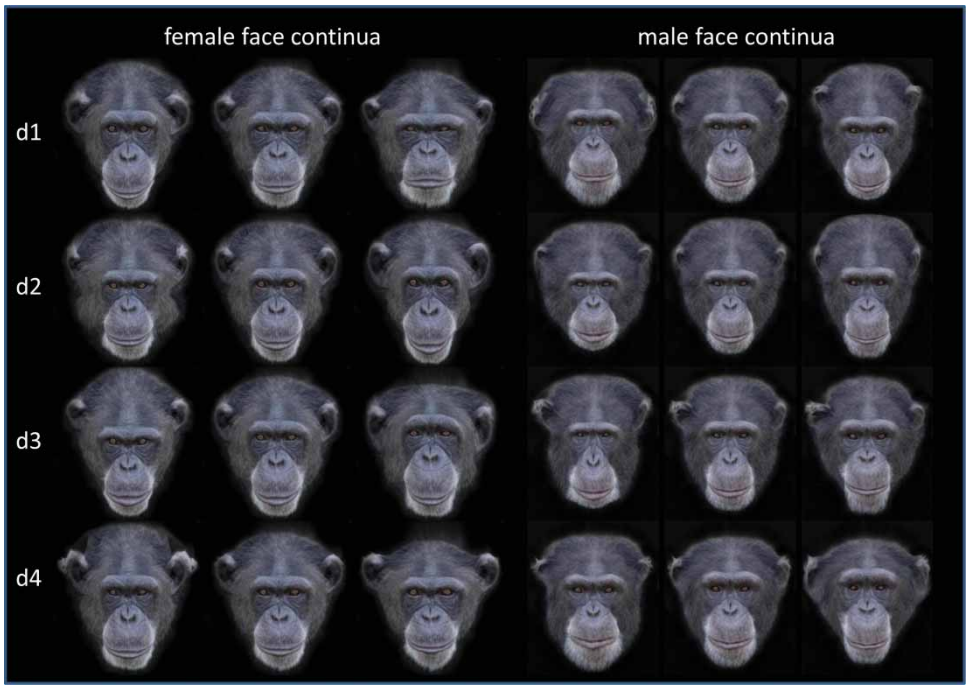

Figure 8. *Visualization of the perceptual dimensions of female and male chimpanzee face space by transforming the population average face into the template space of each of the four high/low dimension averages. To view a colour version of this figure, please see the online issue of the Journal.*

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dimension. In this way, the shape features unique to each dimension could be visualized on an identity-neutral face. The face continua for each dimension were then visually inspected, and prominent differences in facial features were noted. Animations represent the best way to visualize these dimensions, and these can be viewed in the Supplementary material online (http://www.psych-survey.stir.ac.uk/mds_animation/).

Figure 8 illustrates the 1st, 6th, and 11th images in an 11-image continuum (animated in SOM_Figure 1, http://www.psych-survey.stir.ac.uk/mds_animation/) representing the characteristics of each dimension for female chimpanzee faces. Female Dimension 1 (Figure 8, from left to right) appeared to be defined by head width and muzzle tilt. Dimension 2 was defined by an inverse relationship between head width and ear size. Dimension 3 was defined by a head tilt and brow width. Dimension 4 was defined by head height and ear size. For the male chimpanzee face composites, Dimension 1 (Figure 8, from left to right) was defined by head tilt and width, similar to the female Dimension 3. Dimension 2 was characterized by head width and length, creating a rounding of the head. Dimension 3 was characterized by head width and muzzle tilt, similar to female Dimension 1. Finally, Dimension 4 appeared very similar in the male and female chimpanzee faces, an inverse relationship between head and ear size.

Similar to the procedures described for the chimpanzee faces, these high/low dimension averages were symmetrized, the population average transformed into their template space, and animated to illustrate the shape differences defined by each dimension. Figure 9 illustrates the 1st, 6th, and 11th images in an 11-image continuum (animated in SOM_Figure 2, http://www.psych-survey.stir.ac.uk/mds_animation/) representing the characteristics of each dimension for female rhesus monkey faces, where Dimension 1 was defined by an inverse relationship between

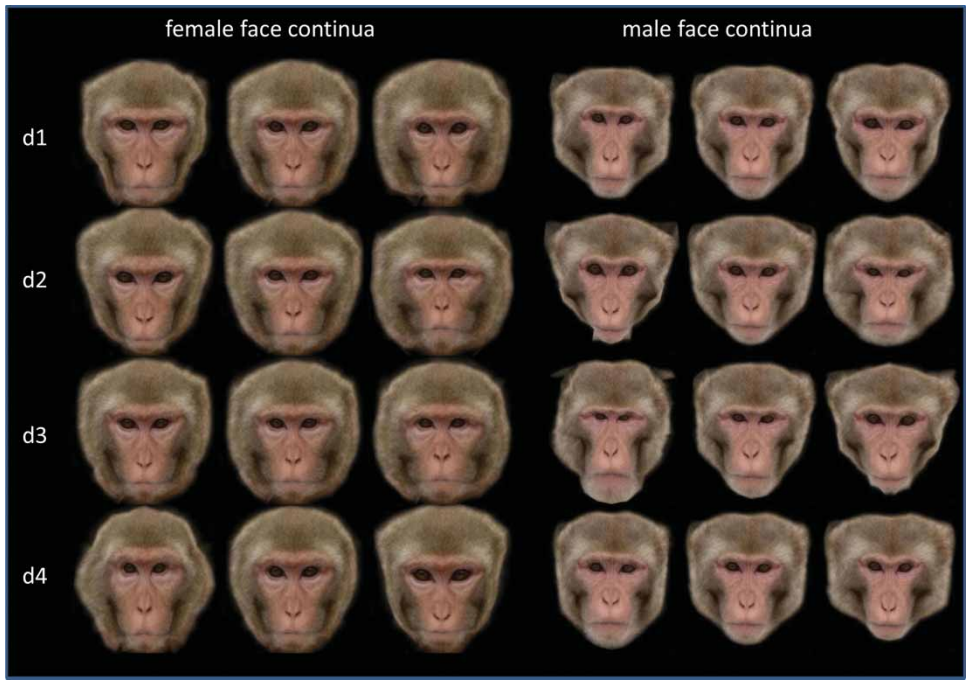

Figure 9. *Visualization of the perceptual dimensions of female and male rhesus monkey face space by transforming the population average face into the template space of each of the four high/low dimension averages. To view a colour version of this figure, please see the online issue of the Journal.*

face size and head width. Dimension 2 was characterized by head tilt, face size, and changes in eye size and interocular distance. Dimension 3 was complex but contained a distinct lifting of the eye corners, nose length, and mouth size. Dimension 4 was defined by a head tilt, mouth width, eye size, and interocular distance. For the male rhesus monkey faces, Dimension 1 was defined by an inverse relationship between head width and face size, similar to female Dimension 1. Dimension 2 was complex but contained a change in lower face width and tilt, nose length, and eye size. Some of this appeared similar to female Dimension 2 but without the overall head tilt. Dimension 3 was defined by an inverse relationship between chin and head size, including a prominent jutting of the chin, eye size, and interocular distance; these latter features were similar to the female Dimension 2. Dimension 4 was defined by an inverse relationship between face size and head width, similar to Dimension 1, but there was an interesting coupling between nose length and brow curvature.

Post hoc analysis of colour

Because the results above suggested that Dimension 1 for both the chimpanzee and rhesus monkey faces may be characterized, in part, by variation in colour, a post hoc analysis was conducted to determine the extent to which colour correlated with any of the four MDS dimensions for the male and female faces of each species. Using the colour picker tool in Adobe Photoshop (Version 7.0), red, green, and blue values were extracted from pixels at two separate locations in each stimulus face, the middle portion of the head, and the centre of the upper lip. These values were then converted into a single hue value using a freely available colour conversion utility (www.ccc.orgfree.com) and were correlated with the derived distance values for each of the four MDS dimensions using Pearson product moment correlations.

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Separate analyses were performed for each gender/species. Lip colour correlated significantly with Dimension 1 for the female chimpanzee faces ($r = .71$, $p < .01$), male chimpanzee faces ($r = .87$, $p < .01$), and male rhesus monkey faces ($r = .74$, $p < .01$), while head colour correlated significantly with Dimension 1 for the male chimpanzee faces ($r = .59$, $p < .01$) and female rhesus faces ($r = .69$, $p < .01$). Colour was not significantly correlated with any of the other three dimensions. Therefore, for both male and female rhesus monkey and chimpanzee faces, colour only played a role in characterizing Dimension 1.

Discussion

This study compared conspecific face processing by chimpanzees and rhesus monkeys by testing specific hypotheses generated by face space theory. Important species differences were observed in both the organization of face space and the feature dimensions used to encode face identity, suggesting that monkeys and apes process conspecifics' faces using different perceptual strategies. The performance of chimpanzees confirmed each of the predicted hypotheses. The population average female chimpanzee face was located closest to the origin of the 2D face space, as derived from the chimpanzees' discrimination performance. The origin of this face space was also the most densely populated region. The average female chimpanzee face was the hardest female face for the chimpanzees to discriminate and was rated least distinctive (most typical) by human chimpanzee experts. In addition, two significant positive correlations were found between the human experts' distinctiveness ratings. These ratings correlated significantly, first, with the chimpanzee's overall performance discriminating these faces and, second, with the vector length describing the location of these faces. The most distinctive female chimpanzee faces were the easiest to discriminate and were located farthest from the origin of face space.

The population average male chimpanzee face was located second closest to the origin of face space, which was also the most densely populated region. It was one of the more difficult faces for the chimpanzees to discriminate, although the male faces were discriminated quite well overall. While the population average male chimpanzee face was rated least distinctive (somewhat typical) by human chimpanzee experts, these ratings did not correlate with the chimpanzees' performance discriminating male conspecifics' faces. Overall, the chimpanzees performed better discriminating the male than discriminating the female conspecifics' faces; however, this failed to reach statistical significance. This high level of performance may explain the lack of significant correlation with the human experts' distinctiveness ratings. Positive correlations, however, were found between the human experts' mean distinctiveness ratings and vector length, indicating that the male chimpanzee faces located closer to the origin of face space were more typical in appearance than those located in the periphery. These results are consistent with previous studies in humans and support the conclusion that typical faces are more difficult to discriminate than distinctive faces because they are located in densely populated regions containing faces that resemble an average (Bruce 1983; Hancock, Bruce, & Burton, 2000; Johnston, Milne, et al., 1997; Rhodes et al., 1987; Valentine, 1991). Overall, these results support strong similarities between the perceptual dimensions important for representing conspecific face identity between chimpanzees and humans—for example, individual identity is encoded on a continuum related to the distinctiveness of specific features, and the average face reflects the central tendency of these features.

The second goal of this study was to identify what specific perceptual features were important for diagnosing individual identity by interpreting the dimensions of face space. Similar approaches utilizing similarity judgements and MDS analyses have been used to study face perception in adult humans for whom the salient dimensions include face shape, hair length, and age and in children for whom the salient dimensions include hair colour, face width, and lip-to-nose ratio (Pedelty et al., 1985). Nishimura and colleagues (2009)

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suggested that children rely on a more restricted set of features to define their face space than adults, with a heavy reliance on a single dimension—for example, eye colour—compared to the multiple dimensions found in adult face perception. Four dimensions best accounted for variation in the chimpanzees' performance discriminating both female and male conspecifics' faces. Through the use of morphing techniques (Nishimura et al., 2009), the shape features accounted for by these dimensions could be visualized on an identity neutral face (the population chimpanzee average face for each gender) and animated (Hancock, 2000, see Supplementary material online). For the female chimpanzee faces, these four dimensions were quite clear and easy to interpret. They represented head width and muzzle tilt, head width and ear size, head tilt, and an inverse relationship between head and ear size. Changes in the shape of the brow also accompanied gross changes to head width in Dimension 1. For the male chimpanzee faces, the dimensions were also quite clear and easy to interpret. They represented head tilt and width, head rounding, head width, and muzzle tilt, and an inverse relationship between head and ear size. There was considerable similarity between the male and female chimpanzee face shape dimensions, and these could be characterized by Euclidean-like perceptual spacing, involving mostly homogeneous changes affecting a small number of discrete features. In addition to these shape features, the two-dimensional MDS plots and post hoc analyses revealed that for both the male and female chimpanzee faces, Dimension 1 could be defined by variations in coloration. In sum, the perceptual dimensions of face space were highly similar for both the male and female chimpanzee faces and could be easily defined by both shape and, to some extent, colour. Presenting the face composites in colour resulted in an uncontrolled variable; however, this method was determined to be preferential due to the ecological salience of colour images and the desire for this study to explore face identity processing in as naturalistic a manner as possible. Such a high degree of similarity in the organization of face space between chimpanzees and humans suggests that the perceptual representation of conspecific face identity shares a recent evolutionary history.

The results were quite different for the rhesus monkeys. For both the male and the female rhesus monkey faces, the population average face was not located close to the origin of face space, but instead appeared in the periphery. Interestingly, the human rhesus monkey experts rated the male and female population average faces as the least distinctive (most typical), but there was no significant correlation between the monkeys' discrimination performance and the human experts' mean distinctiveness ratings, or between these ratings and vector length. The population average monkey faces were easy for the monkeys to discriminate, suggesting that their performance was not affected by the distinctiveness of specific facial features. Similar to the chimpanzee faces, an initial scan of the 2D MDS plot and the post hoc analyses revealed that for both the male and female monkey faces, Dimension 1 could also be defined by colour.

Four dimensions best accounted for the variation in the rhesus monkeys' performance discriminating both female and male faces, and these could be visualized using morphing techniques. Overall, these feature dimensions were more complex (less Euclidean) and more difficult to characterize than those for the chimpanzee faces. This mirrors the results of the face space analysis in that not only was the monkeys' perception of faces uncorrelated with the human experts' perception of their distinctiveness, but it was difficult for humans to interpret these perceptual dimensions from visual inspection alone. For the female rhesus monkey faces, these dimensions appeared to describe an inverse relationship between head width and face size, head tilt and face/eye size and interocular distance, a complex combination of lifting of the eye corners/nose length/mouth size, and head tilt/mouth width, and eye size. For the male rhesus monkey faces, these feature dimensions represented head width and face size, a complex combination of lower face size and tilt/nose length/eye size, head and chin size/interocular distance/eye size, including a prominent jutting of the chin, and face and head width, and a coupling of brow curvature and

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nose length. Each of these dimensions characterized a highly heterogeneous and nonlinear set of features, including more variation of inner facial features, such as eye size, nose length, interocular distance, chin size, and brow shape, than was observed for chimpanzees. This confirms the results of the face space analysis showing that the monkey's performance was not affected by feature distinctiveness—for example, the average face was one of the easiest to discriminate. Although the features characterized by Dimension 1 were very similar between the male and female rhesus faces, the remaining dimensions were quite dimorphic, perhaps explaining why monkeys were better discriminating the male than the female faces. These differences may help explain previous findings from our lab showing that monkeys were significant better in tasks where they were required to discriminate male conspecifics' faces than in tasks with female faces (Parr, Heintz, Lonsdorf, & Wroblewski, 2010).

One explanation for the differences observed in the organization of face space between the chimpanzees and monkeys could lie with stimulus-driven differences. For example, the population average monkey faces that we created may not reflect true representations of the population and thus might explain why the monkey subjects did not perceive them as average. This could have resulted if the individual monkeys included in population averages were somehow atypical or unusual in appearance, or that monkey faces contain a greater amount of variation such that 20 faces were not enough to capture a true average representation. These explanations are unlikely because the averaging technique itself is largely impervious to odd exemplars (Jenkins & Burton, 2011). Also, the faces included in the population averages were taken from monkeys living at the Yerkes Primate Center, where the monkey subjects of this study were born. Therefore, the monkey subjects in this study were familiar with the general facial morphology of stimulus faces, eliminating potential biases due to colony-specific variations in facial morphology—for example, if the monkey faces had come from a different breeding population. Moreover, both the chimpanzee and human monkey experts rated the population average faces as most typical in appearance, so they were not viewed as being atypical or strange in any way. This also suggests that the human experts represented the distinctiveness of both species' faces in similar ways, and analyses showed that overall there were no differences in the distribution of the human experts' ratings for any of the face stimuli. This was an important validation of using human ratings in this study, since it was not possible to have the primate subjects themselves provide the distinctiveness ratings for the face composites.

Although the humans appeared to easily rate the primate faces using a distinctiveness metric, it is quite possible that the perceptual differences reported here for the primate subjects are the result of unique evolutionary adaptations for discriminating the physiognomic properties of each species. If there were greater variability in the physiognomy of rhesus faces than in that of chimpanzees or humans, then most faces would be distinctive and easily discriminated by simple feature detection strategies. However, chimpanzees and humans would benefit from a strategy where subtle changes in a face's physiognomy could be detected by comparison to central prototype. From an evolutionary perspective, such a strategy might work well for monkeys that remain in their groups and can learn the unique features of familiar individuals over a short period of time. However, chimpanzees and humans are characterized by a more complex and flexible social organization known as fission–fusion, where the overall social group size is large, but individuals travel in smaller groups that can change membership over the course of a day or weeks. In this latter arrangement, recognition of individual faces by comparison to a prototype might be more efficient as the social context is malleable. Therefore, it is most likely that the species differences reported here are due to a combination of factors. Differences in physiognomic variation between the two species could have driven the evolution of unique perceptual strategies for processing faces, and differences in social organization may have created the need for a more robust, representational face-processing

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system in chimpanzees and humans than in monkeys. The former question will be examined in future studies using principal components analysis to examine the variation present in faces. Regardless, these data confirm species differences in the representation of conspecific face identity. This finding is consistent with the results of previous studies that report differences in the cognitive specializations underlying face processing in monkeys and apes (Parr, 2011b; Parr, Heintz, et al., 2008; Parr et al., 2000; Parron & Fagot, 2008; and for a review, see Parr, 2011a).

Finally, the present findings should not be viewed as incompatible with several recent studies suggesting norm-based encoding in monkeys for faces and abstract shapes (De Baene, Premereur, & Vogels, 2007; Kayaert, Biederman, Op de Beeck, & Vogels, 2005; Leopold et al., 2006). Leopold and colleagues (2006), for example, presented monkeys with computer-generated human faces and showed that face-selective cells in monkey inferior temporal (IT) cortex were tuned around an average face, such that response amplitudes increased as the faces were morphed from an average towards a caricature. Similar intensity-based changes in neuronal response profiles were found for individual facial features and combinations of features manipulated in schematic faces (Friewald, Tsao, & Livingstone, 2009). These studies utilize a basic face detection paradigm where monkeys are shown many examples of single faces within an experiment. The results are exciting as they provide new and important detail on the response profiles of face-selective neurons when detecting extreme/atypical compared to common features. It is difficult from these few studies alone, however, to conclude the presence of a norm-based face space in monkeys, or that the average face plays a special role in representing face identity. The reported norm-based responses may have occurred as a result of general adaptation to the repeated presentation of face stimuli during the task itself. This could have created a prototype effect around which neuronal responses became tuned as a result of the general adaptive properties of ventral temporal cortex. It has been shown, for example, that when an experiment contains many examples from within a visual category, not restricted to faces, norms can form and change quickly to aid subjects' performance (Panis et al., 2011). Additionally, adaptive coding would predict greater response amplitudes for faces or objects with unusual or extreme features than for those with common features (Baylis, Rolls, & Leonard, 1987; Rhodes & Jeffery, 2006; Rolls, Baylis, Hasselmo, & Nalwa, 1989; Sobotka & Ringo, 1994). In this case, common refers to the frequency of encounters compared to the averageness of the input. Future studies in monkeys should utilize only high-quality images of conspecifics' faces that vary along a complete, norm-based identity trajectory—for example, face to antiface—and examine neuronal responses and perceptual aftereffects to gain a more complete picture of the role of the average face in encoding face identity (Leopold, O'Toole, Vetter, & Blanz, 2001). To conclude, there are many remaining questions about the basic organization of face space in primates, such as how it develops and changes over the lifetime and its neural representation. Nonetheless, the data presented here suggest fundamental differences in the organization of face space and perceptual representation of conspecific face identity in two nonhuman primate species and encourage further study.

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