

Geometric distortions affect face recognition in chimpanzees (*Pan troglodytes*) and monkeys (*Macaca mulatta*)

Jessica Taubert · Lisa A. Parr

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Abstract All primates can recognize faces and do so by analyzing the subtle variation that exists between faces. Through a series of three experiments, we attempted to clarify the nature of second-order information processing in nonhuman primates. Experiment one showed that both chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*) tolerate geometric distortions along the vertical axis, suggesting that information about absolute position of features does not contribute to accurate face recognition. Chimpanzees differed from monkeys, however, in that they were more sensitive to distortions along the horizontal axis, suggesting that when building a global representation of facial identity, horizontal relations between features are more diagnostic of identity than vertical relations. Two further experiments were performed to determine whether the monkeys were simply less sensitive to horizontal relations compared to chimpanzees or were instead relying on local features. The results of these experiments confirm that monkeys can utilize a holistic strategy when discriminating between faces regardless of familiarity. In contrast, our data show that chimpanzees, like humans, use a combination of holistic and local features when the faces are unfamiliar, but primarily holistic information when the faces become familiar. We argue that our comparative approach to the study of face recognition reveals the impact that individual experience and social organization has on visual cognition.

Keywords Visual cognition · Comparative psychology · Face perception · Face recognition

Faces are highly complex visual patterns that contain two types of information. The term first-order information refers to the features that are repeated in every face (i.e. two eyes above a nose above a mouth). First-order information can be used to distinguish faces from other nonface objects. In contrast, second-order information refers to the subtle variation that exists between faces and can be used to distinguish one individual's face from another individual's face. Examples of second-order variation include the metric distance between features (sometimes referred to as “interfeatural relationships” or “configural information”) as well as the surface information (brightness/lighting, color, texture; O'Toole et al. 1999; Rossion 2008). It is well established that humans are highly sensitive to second-order information, and this has led to the notion that humans are face experts, although it remains unclear whether any given relationship between two features is more diagnostic of facial identity than another, or the functional benefits of face expertise (Barton et al. 2001; Goffaux and Rossion 2007; Haig 1984; Rhodes et al. 2006; Sergent 1984). Using second-order information, humans can recognize familiar faces across some transformations and not others. For example, changes in the size and position of a face on the retina are tolerated (Brooks et al. 2002), whereas in plane rotations, e.g. turning a face upside down, are known to have a deleterious effect on recognition (the face inversion effect; Yin 1969). It is generally accepted that inverting a face disrupts holistic processing and, as a consequence, results in a reduced sensitivity to the second-order properties of a face (Goffaux and Rossion 2007; Rossion 2008, 2009).

Familiar human faces are also recognized across other global transformations such as geometric stretching.

J. Taubert (✉) · L. A. Parr
Yerkes National Primate Research Center,
Emory University, Atlanta, GA 30329, USA
e-mail: jtauber@emory.edu

L. A. Parr
Department of Psychiatry and Behavioral Sciences,
Emory University, Atlanta, GA 30322, USA

Stretching, in this context, is a simple affine transformation that has been used to examine the nature of spacing sensitivity in humans, e.g. if a face is stretched, the distance between features is distorted (Hole et al. 2002). In the Hole et al.'s study, subjects were asked to recognize the faces of famous celebrities that were up to 200% wider (horizontal stretch) or 200% taller (vertical stretch) than the canonical images. The authors reported that accurate recognition was robust despite these dramatic spatial distortions and in doing so their results extended what is known about "spacing sensitivity" by concluding that accurate face recognition is unlikely to involve calculating the exact distance between features along the vertical and horizontal dimensions (Hole et al. 2002; also see Bindemann et al. 2008).

Face recognition in nonhuman primates is also characterized by the inversion effect, providing evidence of holistic processing for upright faces (*cotton-top tamarins*, Neiworth, Hassett and Sylvester 2007; *chimpanzees*, Parr et al. 1998; Parr and Heintz 2008; Tomonaga 2007; Tomonaga et al. 1993; *Japanese monkeys*, Tomonaga 1994; *rhesus monkeys*, Dahl et al. 2007; Gothard et al. 2009; Parr et al. 2008; Vermeire and Hamilton 1998). An outstanding question, however, is whether all primates use the same second-order information to recognize faces. Parr et al. (2006) reported that chimpanzees were sensitive to second-order information when the spatial location of facial features were rearranged, but using the same stimulus manipulation, rhesus monkeys were insensitive to changes in second-order features (Parr et al. 2008). Dahl et al. (2007) found that rhesus monkeys were able to detect the differences between faces in which the spacing between the eyes had been altered, and, using a similar visual preference task methodology, Sugita (2008) showed that sensitivity to the spacing of features and the identity of those features did not require any visual experience with faces from birth.

At present, it is not known whether some second-order relationships are more diagnostic than others and thus make a disproportional contribution to face recognition or whether the same relationships remain diagnostic across different species. Given that the faces of different primate species differ dramatically, it would not be surprising if the source of individual variation was somewhat species-specific. Comparative studies across nonhuman primate species are rare but are essential to understand how face recognition is achieved in other primates and how these processes are similar to or different from humans. The current experiments examined whether, in addition to being orientation-specific, face recognition in nonhuman primates tolerates other geometric distortions. Specifically, we tested whether face recognition in nonhuman primates tolerates geometric stretching in a series of three experiments in

which subjects performed a simultaneous match-to-sample task in which they were required to discriminate familiar and unfamiliar faces that varied in the quality of their second-order information.

Experiment one

In our first experiment, we investigated the effects of two global transformations on face matching: horizontal stretching and vertical stretching. These transformations are global in the sense that they transform the entire image. If individual recognition of a face relies on global measurements across the entire face, then stretching will impair performance since the exact distances between features will be altered. Both a vertical and a horizontal condition were included because each selectively distorts a different subset of interfeatural relations and our primary aim was to determine whether horizontal and vertical relations contribute equally to accurate face recognition. The task was given to both chimpanzees and rhesus monkeys to address inconsistencies in the literature regarding the ability of monkeys and apes to utilize second-order configural information. A control condition, where subjects were simply asked to discriminate between the faces of two conspecifics, was included to compare with the geometric test conditions. If the vertical distances between features are critical to overall performance in either species, then this would manifest in behavior as a significant drop in accuracy relative to performance in control trials. The same hypothesis applies for the horizontal distances between features.

Method

Subjects

Six chimpanzees (*Pan troglodytes*; four male) served as subjects together with six rhesus monkeys (*Macaca mulatta*; two male). The chimpanzees were between 15 and 22 years of age at the time of testing. All six chimpanzees were captive born and raised in a nursery with peer contact. The monkeys were between 8 and 9 years at the time of testing. All monkeys were reared in large social groups before being relocated to the Yerkes main station (Atlanta, GA) at 3–4 years of age. Prior to these experiments, all 12 subjects had participated in multiple studies where their face discrimination skills had been tested (Parr et al. 2000, 2006; Parr and Heintz 2008; Parr et al. 2008; Taubert and Parr 2009). The feeding schedule for these animals was not disrupted by test sessions. Food and water was available ad lib.

Apparatus

The apparatus used to test subjects had been described in detail elsewhere (Parr et al. 2006, 2008). For the chimpanzees, the computerized system consisted of a personal computer, a 19-inch monitor and a joystick. Reinforcement was delivered by hand. For the monkeys, on the other hand, the computerized system included a 13-inch touch screen monitor (no joystick), and reinforcements were distributed by an automated pellet dispenser.

Stimuli

Sixty high-quality digital images were used to generate a stimulus set comprised of thirty chimpanzee and thirty monkey faces, prepared using Adobe photoshop CS2 software (see Fig. 1a). For each species, 15 of these were used to create the matching pair and 15 were the mismatching images. The subjects were already familiar with these exact images from a previous experiment (Parr, *submitted*). Each photograph was resized to 350 pixels in height and aligned along the horizontal axis. After these standardized stimuli were converted into grayscale (256, 8 bit), an opaque black mask around the external outline of each face was added to remove the background information (See Fig. 1a). The vertically stretched stimuli were created by applying a geometric transform to each of the original stimuli that increased their height by 150% (see Fig. 1a). As a result of this affine transformation, the vertical relationships that existed between facial features were stretched, but the horizontal relations remained the same. The procedure that produced the horizontally stretched stimuli was identical to the vertical stretch procedure except it was the width of the original stimuli that was increased by 150% (see Fig. 1a). Thus, there were three sets of trials (15 original controls, 15 horizontally stretched and 15 vertically stretched) included in the experimental task.

Procedure

Subjects were tested in their home cages using a simultaneous match-to-sample (MTS) procedure. All subjects had extensive experience discriminating faces and other visual images using this paradigm (Parr et al. 2000, 2006, 2008; Taubert and Parr 2009). Each MTS trial began when a sample stimulus (a whole face) appeared on one of the four sides of the computer monitor. The subject was then required to make an orienting response toward the sample. The chimpanzees used the joystick to position a white cursor above the sample. The monkeys were required to touch the sample three times in rapid succession. Immediately following the orienting response, two comparison stimuli appeared on the opposite side of the screen at an equal

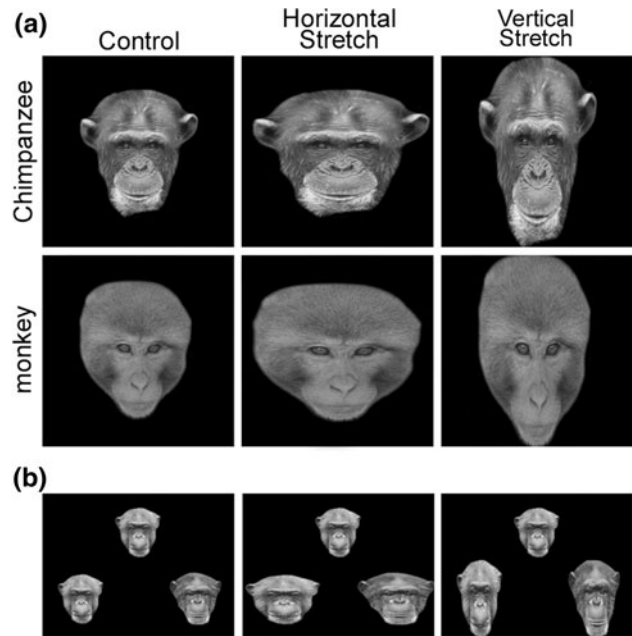


Fig. 1 **a** The experimental stimuli used in Experiment one. **b** An example of a trial from each of the three geometric conditions (*control*, *horizontal stretch* and *vertical stretch*). In each example provided, the sample appears at the top of the display with the two comparison stimuli below. The correct choice is on the *left*, and the same foil appears on the *right*. The position of target and foil was counterbalanced

distance from the sample. A correct choice was recorded when a subject directed their next response toward the comparison stimulus that was the same face as the sample using the joystick or the touch screen panel. This would result in a high-pitched tone and the delivery of a food reward. Directing a response toward the mismatching image or foil (a different face from the sample) was recorded as an incorrect response and resulted in a low tone. There was no food reward when the subject's choice was incorrect.

Subjects were first trained on the 15 untransformed control face trials. These were repeated three times (45 trials in total) in a daily session. These were presented in a pseudo-random order such that each trial was presented once before any trial was repeated. The position of the match relative to the foil was determined at random. Testing on the 15 control trials continued until performance exceeded 85% accuracy in a single session. After reaching this criterion, the geometrically transformed trials were added so that the task contained 45 unique trials, the 15 previously learned matching trials, together with 15 vertically and 15 horizontally transformed trials. In the geometrically transformed trials, the sample was the original canonical image, and the two comparison stimuli contained the manipulation (see Fig. 1b). An accurate response would, therefore, require the subjects to tolerate the geometric distortion of the previous sample.

Data analysis

First, the performance of monkeys and chimpanzees on control trials was compared to verify that subjects were performing similarly in the MTS procedure. Next, a series of discrete a priori planned comparisons were used to examine the effect of the stretch manipulations on performance compared to that species' control trial performance. Alpha level was corrected for multiple comparisons using the Bonferroni rule, $\alpha = 0.05/\#$ comparisons. For this initial experiment, the adjusted alpha was 0.025 as there were two planned comparisons, control versus horizontal stretch and control versus vertical stretch.

Results and discussion

On average, the monkeys needed more training sessions (blocks of 45 control trials) before reaching the criterion ($M = 9.83$, $SEM = 2.27$) than the chimpanzees ($M = 5.83$, $SEM = 2.04$); however, an independent samples t -test showed this difference not to be significant ($t_{10} = 1.31$, $P = 0.14$).

Two paired t -tests were conducted for each species to determine whether either of the stretch conditions had a significant impact on performance compared to control trials (no stretch manipulation) (see Fig. 2). Chimpanzees performed significantly better on the control trials than on the horizontal stretch trials ($t_5 = 2.98$, $P = 0.01$), but they were tolerant of vertical stretching ($t_5 = 1.93$, $P > 0.1$). In contrast, the monkeys showed no evidence of a significant difference between performance on control trials compared to the horizontal stretch trials ($t_5 = 1.61$, $P = 0.11$) or the vertical stretch trials ($t_5 = 1.25$, $P = 0.14$).

Experiment two

In Experiment one, both species were tolerant of vertical stretching, a linear transformation that altered the vertical dimension of the experimental stimuli, but only chimpanzees showed a significant impairment matching the horizontally stretched faces consistent with our main hypothesis that facial identity is conveyed by different kinds of second-order cues dependent on species. However, these results raise several additional questions. How, for example, were subjects able to match an unaltered face to the correct vertically stretched stimulus and why did horizontal stretching disproportionately impair chimpanzee's face matching performance when compared to rhesus monkey's performance?

In the face recognition literature, there is a longstanding proposal that faces are processed holistically, integrating

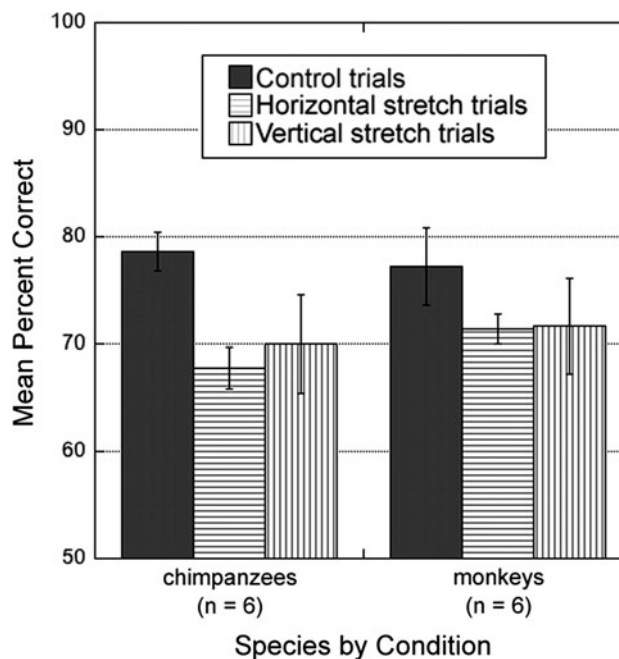


Fig. 2 Mean percent correct, for chimpanzee and monkeys in control, horizontal stretch and vertical stretch trials (error bars = ± 1 SEM)

information about multiple features and their relative spacing together into a single indivisible unit (Rossion 2008; 2009; Tanaka and Farah 1993; Young et al. 1987). However, there is no reason to believe that all interfeatural relationships contribute equally to the recognition process, an assumption supported for chimpanzees by the results of Experiment one. Information diagnostic to face recognition may differ for each species. These data imply that chimpanzees are more sensitive to the disruption of horizontally arranged features compared to vertically aligned features. Hole et al. (2002) also reported that their human subjects were less accurate when recognizing famous faces that had been horizontally stretched in the first of their experiments. The reason why horizontally stretched faces are registered as different identities is open to speculation, but one possibility may be that horizontal relations are more diagnostic of facial identity than vertical relations. More important, however, is the observation that the rhesus monkeys did not share the same sensitivity to horizontal stretching as the chimpanzees. This result is suggestive of interesting species differences in the source of second-order variation that contributes to face discrimination, a difference that has already been supported by a number of studies (Neiworth et al. 2007; Parr et al. 1998, 2006, 2008; Tomonaga 2007; Tomonaga et al. 1993; Vermeire and Hamilton 1998; Yin 1969).

However, our presumption thus far has been that geometric stretching selectively distorts the distances between features that are used to diagnose identity. In light of the observation that these distortions did not alter the performance of rhesus monkeys, an alternative explanation

for the results of Experiment one is that rhesus monkeys are not sensitive to the spacing of features extracted from a global representation and instead utilize local information about the shape of individual features. To examine this hypothesis more specifically and to provide further insight into the nature of face recognition in nonhuman primates, Experiment two presented subjects with a modified stretch manipulation in which the comparison stimuli were only partially stretched (top stretch or bottom stretch), thus preserving the identity of local features delegated to the upper and lower halves of the face (see Hole et al. 2002). If the subjects can use feature information to match faces, then they should perform well on nonglobal stretch trials regardless of which half has been distorted. We also added two part conditions (top part and bottom part) to test whether performance would recover when conflicting information was removed from the sample. We reasoned that if the subjects were using features to match faces in the nonglobal trials, then they would also be able to match features in a half-face sample to a nonglobal stretch target.

Experiment 2a: method

The subjects and apparatus used were precisely the same for Experiments one.

Stimuli

The stimulus sets used in Experiment 2a were generated from photographs taken of 80 novel individuals (40 chimpanzees and 40 rhesus monkeys). Of the forty chimpanzee faces, twenty were randomly selected to be part of the control trials (ten matches and ten foils). The preparation of the control stimuli was identical to Experiment one. The top stretch faces were produced by horizontally dividing each of the twenty faces into two halves along the horizontal midline and then vertically stretching the top half till this region was 150% taller than its original size. The width was left unaltered. The same process was also applied to the bottom half of each unaltered face to produce the bottom stretch faces. Examples of these stimuli are shown in Fig. 3a. To create the top part stimuli, the bottom halves were removed from the top stretch faces. Likewise, the top half of every bottom stretch stimulus was removed to create the bottom part stimuli (also see Fig. 3a). Thus, there were five types of test trials in total (control, top stretch, bottom stretch, top part and bottom part).

Procedure

In Experiment 2a, the subjects were not given any training with the stimuli before adding the manipulated trials. This

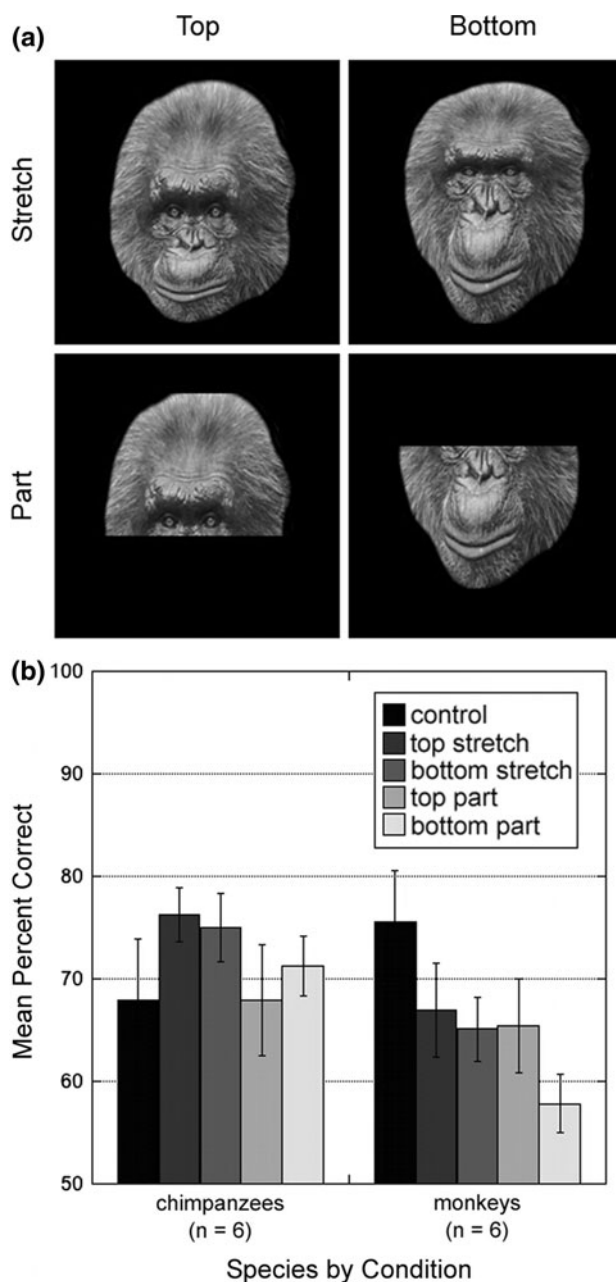


Fig. 3 **a** The experimental stimuli used in Experiment 2a. **b** The results of Experiment 2a; mean percent correct across the five experimental conditions (error bars = ± 1 SEM)

change in pre-experimental procedure was intended to increase task difficulty and discourage any learned strategies for matching stretched faces. Regardless of the species being tested, in a single session, the subjects were required to match ten control faces against ten foils. Interleaved with the control trials were 40 stretch trials (10 top stretch, 10 bottom stretch, 10 top part and 10 bottom part). Trial order was randomized. When presented with a bottom stretch trial, the subject was asked to match an unaltered face to the bottom stretch equivalent. The same was true in a top

stretch trial except the correct match had undergone the top stretch transformation. The part trials (top part and bottom part) differed from the nonglobal stretch trials in that the sample provided the subject with a limited amount of information. Effectively, the subjects were asked to match the top half of a face to the correct top stretch face or the bottom half of a face to the correct bottom stretch. Subjects received only 4 sessions of these trials, where each trial was seen twice in a single session.

Experiment 2a: results and discussion

As in Experiment one, control performance was first compared across species using an independent samples *t*-test. Based on accuracy in control trials, there was no evidence of differential performance across species ($t_{10} = 0.99$, $P = 0.31$) although we note that, on average, chimpanzees ($M = 67.9$, $SEM = 5.5$; see Fig. 3b) were less accurate than monkeys ($M = 75.6$, $SEM = 5.5$; see Fig. 3b).

The 2×5 ANOVA model was then used to test whether the experimental conditions mediated subject accuracy. Although there was also no evidence of significant variation between the five levels of the repeat factor condition ($F_{4,40} = 1.89$, $P = 0.13$), there was a significant interaction between species and condition indicating that the two species had performed differently across the five experimental conditions ($F_{4,40} = 3.24$, $P = 0.02$; see Fig. 3b). To follow-up this interaction, the four manipulated trials were compared to control trials for each species using paired *t*-tests. For each species, the first analysis examined whether information in each region of the face contributed differentially to performance. Thus, the two nonglobal stretch trials were compared, and the two parts trials were compared. If no differences were found, then the performance on these two manipulations were averaged across face parts and compared to control trials. The Bonferroni rule was used to adjust the alpha level for each species ($\alpha = 0.0125$).

For the monkeys, an initial comparison between the two nonglobal conditions (top stretch versus bottom stretch) revealed no significant difference across these two conditions ($t_5 = 0.75$, $P = 0.46$). However, when both nonglobal stretch conditions were averaged together and compared to the control condition, it was revealed that monkey's performance was significantly impaired by nonglobal stretching ($t_5 = 2.49$, $P < 0.01$; see Fig. 3b). This impairment rules out a feature-based account for the results of Experiment one. Matching features in the two part trials was also more difficult for monkeys than matching whole faces in the control trials ($t_5 = 3.61$, $P < 0.01$; see Fig. 3b) with no significant differences observed between the top part and bottom part trials ($t_5 = 1.46$,

$P = 0.17$). This second result is also inconsistent with feature-based processing and strongly suggests that rhesus monkeys extract second-order information from holistic representations of faces.

On the other hand, when the data from chimpanzees were analyzed, a different pattern of results was revealed. When the two nonglobal stretch conditions were averaged together ($t_5 = 0.5$, $P = 0.35$), a comparison between the nonglobal stretch trials and control trials indicated that chimpanzees were *more* accurate in nonglobal stretch trials than in control trials ($t_5 = 2.0$, $P < 0.01$; see Fig. 3b). Moreover, when the part trials were averaged together ($t_5 = 0.63$, $P = 0.11$) and compared with control trials, there was no difference evident between part trials and control trials ($t_5 = 0.43$, $P = 0.07$; see Fig. 3b). Thus, chimpanzee's performance in the control trials was relatively poor when compared to other trial types, and this did not differ from performance matching parts of a face. Humans also experience considerable difficulty matching and remembering unfamiliar faces (Bruce et al. 1999, 2001; Burton et al. 2005). This has led researchers to conclude that the underlying processes by which human faces are recognized are qualitatively different for familiar and unfamiliar faces. For example, Bruce and Young (1986) suggest that unfamiliar face recognition relies on image-based cues, whereas familiar face recognition engages a type of processing that transcends any particular image and tolerates superficial changes in lighting, context and viewpoint (also see Hancock et al. 2000). The dissociation between familiar and unfamiliar face recognition may be reflected by the relative importance of features. Humans tend to depend more on feature information when a face is unfamiliar than when a face is familiar (Bruce et al. 1999; Clutterbuck and Johnson 2002; Megreya and Burton 2006; Megreya and Binde-mann 2009). What the results of Experiment 2a may imply is that chimpanzees, like humans, use different sources of information to perform face recognition tasks depending on familiarity and that this shift in strategy is not present for rhesus monkeys. A lack of pre-experimental familiarity with the stimulus set may, therefore, explain why chimpanzees were able match features in Experiment 2a. To test this hypothesis, the same conditions were repeated in Experiment 2b following the completion of a training phase designed to increase pre-experimental exposure to the visual stimuli. The expectation was that both chimpanzees and monkeys would find the nonglobal stretch and part trials more difficult than control trials.

Experiment 2b: method

The same twelve subjects that were tested in all previous experiments participated in Experiment 2b.

Stimuli and procedure

The visual stimuli were novel photographs taken of 20 chimpanzees and 20 rhesus monkeys that had been seen in previous experiments. It is important to note that these images were novel, as in Experiment 2a; however, they depicted experimentally familiar individuals that had been matched in previous experiments (including Experiment one). For each species, 10 faces were chosen at random to be the samples (and targets) in both training and test phase. The remaining 10 photographs became the foils. The subjects were required to reach criterion (>85%) in a single training session before testing began. The structure of the test sessions was the same as in Experiments 2a and 2b. The only exception being the control trials in the current experiment did not depict a unique set of exemplars.

Experiment 2b: results and discussion

The results of Experiment 2b are presented in Fig. 4. As in Experiment 2a, the chimpanzees were as accurate as the rhesus monkeys in control trials ($t_{10} = 0.49$, $P = 0.57$). However, in Experiment 2b, the subjects were given the opportunity to become familiar the experimental stimuli prior to testing and, therefore, it was expected that the factor known as *condition* (comparing control trials, top stretch, bottom stretch, top part and bottom part) would be significant with no interaction between species. As predicted, the 2×5 ANOVA revealed a significant main effect of condition ($F_{4,40} = 7.15$, $P < 0.01$). In accordance with the experimental hypotheses, it was first confirmed that the source of the variance was not between the two nonglobal stretch conditions ($t_{11} = 1.82$, $P = 0.10$) nor the two part conditions ($t_{11} = 0.92$, $P = 0.37$). The two nonglobal trials were the averaged together and compared to control performance to demonstrate that nonglobal stretching impaired face recognition ($t_{11} = 3.67$, $P < 0.01$). A similar difference (in both direction and significance) was also evident between the part and control trials ($t_{11} = 5.76$, $P < 0.01$). The interaction between species was not significant in Experiment 2b suggesting that pre-experimental familiarity had had an effect on chimpanzee's performance ($F_{4,40} = 0.92$, $P = 0.46$; see Fig. 4).

Discussion

Our principle aim in this paper was to clarify the nature of second-order information in nonhuman primates, and we have done so in several important ways. First, the data collected in Experiment one confirm that chimpanzees and monkeys tolerate some geometric stretching when matching

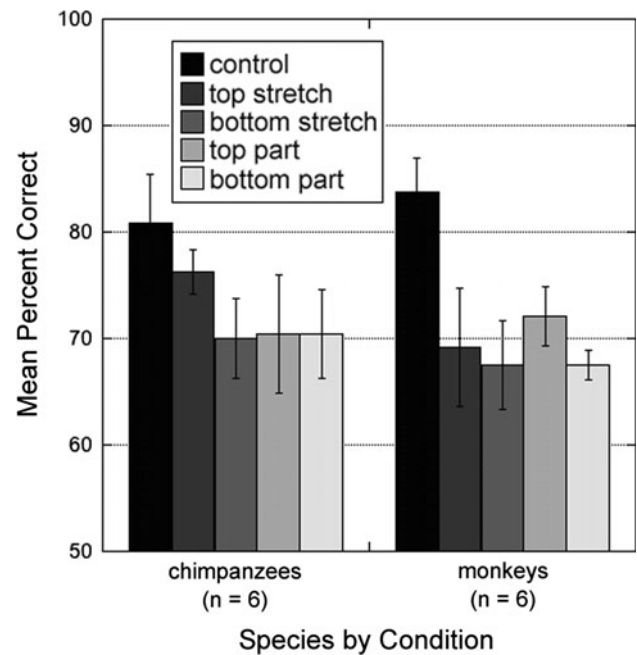


Fig. 4 The results of Experiment 2b; mean percent correct across the five conditions (*error bars* = ± 1 SEM)

familiar faces, which means that the term “second-order information” is unlikely to refer to absolute distances between features. For chimpanzees, familiarity is a critical factor for accessing second-order information from a holistic representation, as reflected by the difference between the results of Experiments 2a and 2b. When chimpanzee faces were unfamiliar, subjects used the shape of features to match the sample to the target resulting in better performance in the nonglobal trials. We argue that great apes show a bias against unfamiliar faces whereby subjects adopt a somewhat inefficient discrimination strategy that is based on features, a claim for which there is support from studies in human behavior (Bruce et al. 1999; Clutterbuck and Johnson 2002; Megreya and Burton 2006; Megreya and Bindemann 2009) and electrophysiological recordings (Bentin and Deouell 2000). These data highlight the limitations of formulating general theories about face recognition in nonhuman primates based on the results of tasks when the level of familiarity subjects have with the experimental stimuli is not known. Similarly, in the future, researchers should consider any previous participation in cognitive experiments as an important factor in the outcome of an experiment.

Although possible, it is also unlikely that chimpanzees do not build holistic representations for unfamiliar faces. First, there is ample evidence in the human literature that the markers of holistic processing are present for unfamiliar faces (Goffaux and Rossion 2006; Hole 1994; Le Grand et al. 2004). Second, in Experiments 2a and 2b, the chimpanzees continued to show poor performance in part trials compared to other trial types. This finding demonstrates

that chimpanzees have difficulty matching part of a face to a whole face, regardless of whether faces are familiar or unfamiliar. This result is consistent with holistic processing because it demonstrates that the presence of a global face changes the perception of the local features. The part-whole effect has become a standard marker of holistic processing in the human face recognition literature (Davidoff and Donnelly 1990; Tanaka and Sengco 1997; Tanaka and Farah 1993). The data from these experiments, therefore, are consistent with previously reported evidence of holistic face processing in great apes (Parr et al. 2006; Young et al. 1987). So what, then, changes as a face becomes familiar? Perhaps what changes is sensitivity to the second-order properties that are contained within a holistic representation. Thus, apes are only in a position to take full advantage of holistic processing following a considerable amount of exposure to any particular face.

Although counter-intuitive, these data not rule out the possibility that the chimpanzees used an entirely different strategy in Experiment 2b that was based on a pictorial code rather than a mental representation and, as a result, their performance was extremely vulnerable to image manipulation. This seems unlikely because increased practice with the experimental manipulation, if anything, should result in the development of a processing heuristic that allowed for increased overall performance, which was not the case. For chimpanzees, chronological order does not reflect an over-increase in performance and, thus, we argue that the result in Experiment 2b reflects holistic interference.

This paper also makes an important contribution to a large existing literature by revealing differences in how accurate face recognition is achieved in apes and monkeys. Evidence of a global-to-local interference in Experiment 2a and 2b is consistent with previous claim that rhesus monkeys build holistic representations of faces (Dahl et al. 2007; Taubert and Parr 2009). However, the second-order properties that are extracted from these representations and used to diagnose identity may be different across the primate order (Experiment one). These data alone cannot define the second-order information that is used by monkeys to diagnose identity, but in Experiment one, we present evidence that rhesus monkeys are less sensitive to horizontal dimensions than humans (Hole et al. 2002; Bindemann et al. 2008) or chimpanzees (Experiment one). Keeping in mind that the results presented here are based on a small sample of twelve subjects, there is genuine theoretical progress to be made by investigating what kinds of information are most useful for diagnosing identity across species.

Finally, in Experiment 2a, we found evidence of holism associated with unfamiliar face recognition in monkeys. The implication is that there is no qualitative shift as an unfamiliar face becomes familiar, whereas chimpanzees require experience with an individual's face before they

build a holistic representation. The first explanation we offer is that monkeys might not be able to easily decompose visual objects into smaller local components and, thus, do not have feature information available to them. In related research, there is evidence that rhesus monkeys perceive global content before the local details of hierarchical displays (Sripati and Olson 2009). However, at present, there is no reason to believe that perceptual binding is stronger in monkeys than in apes.

An opposing account considers the profound influence that social interactions have on cognitive development. Human and chimpanzee societies are characterized by fission–fusion dynamics and, as such, an individual can encounter countless faces throughout their lifetime. Many of these faces will only be seen once, and while it remains important to detect an unfamiliar face and register any signal that communicates the intent to interact, it would be very costly to analyze and encode every face at the individual level. In this way, feature-based strategies might be relied upon until there has been sufficient exposure to warrant the use of global second-order properties, such as the spaces between features. In contrast, rhesus monkeys form relatively stable social groups. As such, perhaps they lack the tendency to use feature-based heuristics because the likelihood of encountering someone that will not be seen again is low. This account squares with the general lack of face expertise in rhesus monkeys that has been observed in previous face recognition studies (Parr and Heintz 2008; Parr et al. 2008; Taubert and Parr 2009).

In short, the findings of the present study are consistent with the assertion that, despite gross similarity, primates can discriminate between the faces of conspecifics using second-order information but they also contradict the popular presumption that second-order information is uniform across the primate order. Instead, we conclude that while first-order information is highly conserved across species (the course organization of facial features, e.g. two eyes above a nose above a mouth), second-order information is species-specific and how that information is used may well depend on individual development within any given social structure.

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