
Effect of familiarity and viewpoint on face recognition in chimpanzees

Lisa A Parr, Erin Siebert[¶], Jessica Taubert[¶]

Department of Psychiatry and Behavioral Sciences, Center for Translational Social Neuroscience, Emory University, Atlanta, GA 30322, USA; [¶] and Yerkes National Primate Research Center, Emory University, 954 Gatewood Road, Atlanta, GA 30329, USA; e-mail: lparr@emory.edu

Received 29 March 2011, in revised form 27 June 2011; published online 1 September 2011

Abstract. Numerous studies have shown that familiarity strongly influences how well humans recognize faces. This is particularly true when faces are encountered across a change in viewpoint. In this situation, recognition may be accomplished by matching partial or incomplete information about a face to a stored representation of the known individual, whereas such representations are not available for unknown faces. Chimpanzees, our closest living relatives, share many of the same behavioral specializations for face processing as humans, but the influence of familiarity and viewpoint have never been compared in the same study. Here, we examined the ability of chimpanzees to match the faces of familiar and unfamiliar conspecifics in their frontal and 3/4 views using a computerized task. Results showed that, while chimpanzees were able to accurately match both familiar and unfamiliar faces in their frontal orientations, performance was significantly impaired only when unfamiliar faces were presented across a change in viewpoint. Therefore, like in humans, face processing in chimpanzees appears to be sensitive to individual familiarity. We propose that familiarization is a robust mechanism for strengthening the representation of faces and has been conserved in primates to achieve efficient individual recognition over a range of natural viewing conditions.

1 Introduction

Objects in the real world must be recognized across a range of different viewing conditions. How this is accomplished remains an important question for the cognitive and visual sciences. Most common objects are typically encoded at the basic level which maximizes the differences between category exemplars, eg chair versus shoe. Object-centered theories propose that this is accomplished by comparing the structural properties of objects, the identity of, and relationship between, their component elements, to a stored, 3-D object-centered, representation (Biederman 1987). As long as the objects can be decomposed into component elements that are visible and categorically distinctive, recognition will be independent of viewpoint. Face recognition, however, poses a special problem for object-centered theories as categorization occurs at the subordinate level, which maximizes the differences between exemplars of the same category and enables the recognition of faces at the individual level, eg John versus Ted (Diamond and Carey 1986; Maurer et al 2002; Mervis and Rosch 1981). Because all faces contain the same component elements—eyes, nose, and mouth, arranged in the same general configuration—subordinate-level face categorization cannot be accomplished simply by identifying differences in component elements and their spatial arrangement. Alternatively, view-centered theories suggest that faces and objects are recognized by a 2-D interpolation of different views and recognition occurs when the input view matches a stored view (Bülthoff and Edelman 1992; Poggio and Edelman 1990; Tarr and Pinker 1989). Inherent in this account is that face recognition is viewpoint-dependent: our success in recognizing a specific face is enhanced by our experience with multiple views of that face.

The importance of familiarity and viewpoint for face recognition in humans has been highlighted by several studies. Here, facial viewpoint refers to changes in face orientation along the vertical axis, eg frontal to profile view. While it is well-known that in-plane rotations, eg inverting a face 180°, result in impaired recognition of both

familiar and unfamiliar faces (Johnston and Edmonds 2009; Rossion 2008; Valentine 1988; Yin 1969), changes in facial viewpoint appear to selectively impair the ability to recognize unfamiliar faces (Bruce 1982; Hancock et al 2000; Hill et al 1997; Johnston and Edmonds 2009; McKone 2008). It has even been suggested that two different unfamiliar faces presented in the same view may appear more perceptually similar to one another than the same face presented across two different views (Favelle et al 2007; Taubert et al 2010). These findings have led to the suggestion that unfamiliar faces are processed in a viewpoint-dependent manner, ie recognition is dependent on the viewpoint encountered, whereas familiar faces are processed in a more viewpoint-independent manner, ie recognition survives changes in facial viewpoint. Familiarity is extremely important for face recognition as it enables the formation of robust representations of different individuals so that recognition can survive the broad range of viewing conditions present in everyday encounters (Hancock et al 2000).

Familiarity itself, however, does not guarantee viewpoint-independence for faces. Troje and Kersten (1999) used a clever manipulation to disentangle the influence of familiarity and viewpoint by presenting frontal and profile photographs from two categories of familiar faces: work colleagues who are frequently encountered across a range of viewpoints and the subject's own face. While the latter is highly familiar, its viewpoint is restricted in that we most often encounter our frontal reflection in a mirror. Overall, the authors found that people were much faster at recognizing their own face than their colleagues' faces, but recognition of colleagues' faces was much more tolerant of a viewpoint change. Similarly, researchers have reported better performance recognizing faces across in-depth rotations compared to pitch rotations, looking up or looking down, and performance was better for pitch rotations of an upward compared to downward rotation (Favelle et al 2007). This also supports the finding that face recognition is highly dependent on one's experience with different viewpoints. Most people have more experience with faces rotated in-depth than in-pitch, and for faces rotated up (looking from below) than rotated down (unless you are very tall!). These studies suggest that it is not familiarity per se, but familiarity across a range of viewpoints that is important for robust face recognition to develop.

Understanding the evolution of face processing specializations in humans, such as the importance of familiarity and viewpoint to face recognition, has gained considerable interest over the past decade, particularly in light of recent studies that suggest differences in the face-processing skills of monkeys and apes (see Parr 2011). However, the vast majority of these studies have presented only single viewpoints of unfamiliar faces. In one of the first studies of its kind, researchers showed that, after training, rhesus monkeys could recognize a conspecific's face across a variety of transformations, including size, illumination, color, and facial viewpoint (Rosenfeld and Van Hoesen 1979). Many years later, Parr et al (2000) used a matching-to-sample (MTS) task to show that chimpanzees were rapidly able to match two different views of the same chimpanzee's face. While the performance of rhesus monkeys on the same task was initially quite poor, they were eventually able to learn the task (Parr et al 1998, 2000). Gothard et al (2009) used eye-tracking in combination with a visual paired comparison task to examine how rhesus monkeys scan unfamiliar faces. The monkeys were first habituated to two different viewpoints of the same monkey and then, in the test phase, they were presented a third view of the familiarization monkey plus a novel conspecific. Subjects tended to look longer at the novel monkey's face than the novel viewpoint of the familiarized monkey, demonstrating that subjects could recognize the same individual across a change of viewpoint (Gothard et al 2009).

Only one study has varied familiarity and viewpoint in the same study. Capuchin monkeys (*Cebus apella*) were required to discriminate familiar (in-group) and unfamiliar (out-group) conspecifics' faces using an oddity paradigm in which subjects were rewarded

for choosing the 'odd' image in a four-image array (Pokorny and de Waal 2009). After a short training phase, subjects were presented with an array of four different photographs, three of which showed different viewpoints of the same individual, while the fourth image showed a different monkey. Subjects performed well in this test, demonstrating good individual recognition skills. Unlike humans, however, no strong advantages were found for familiar versus unfamiliar individuals (Pokorny and de Waal 2009). Using a broad band of methodologies, these studies provide evidence that individual recognition in monkeys and chimpanzees is tolerant of a viewpoint change; however, it remains unclear how familiarity affects this skill. Social interactions in large primate groups would be significantly aided by the ability to recognize specific individuals despite atypical or impoverished viewing conditions.

Methodological limitations may explain why familiarity is not often included as a variable of interest in face-processing studies. The majority of subjects used in cognitive studies, for example, live in pairs or small groups and the presence of cage bars limits clear photography. Therefore, acquiring enough photographs of familiar individuals may not be possible. We examined here the influence of familiarity and viewpoint on the ability of chimpanzees to match conspecifics' faces. Over the last 15 years, the subjects of the present study have participated in numerous projects examining face recognition using photographs taken from chimpanzees living at either the Yerkes National Primate Center's field station, or the MD Anderson Cancer Center in Bastrop, TX. These individuals are personally unfamiliar to the subjects, ie they have never encountered each other in real life, but, through exposure to numerous photographs over the course of testing, they have become familiarized in a manner similar to the way famous human celebrities become familiarized through the media. We hypothesized that chimpanzees' performance matching unfamiliar faces would be more impaired across a change in viewpoint than the familiarized faces. These data will provide important information about the specific role of familiarity in face recognition and, more generally, about the comparative nature of face recognition in primates.

2 General methods

2.1 Subjects

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

2.2 Stimuli

Stimuli consisted of high-quality digitized images of conspecifics' faces presented on the computer using a stimulus height of 300 pixels and 150 dpi. All images were presented in 256 gray-scale and edited so as to exclude background information. The familiar stimuli consisted of images of chimpanzees living at the Yerkes Primate Center field station, and the MD Anderson Cancer Centre in Bastrop, TX. While the subjects in this study did not know these individuals personally, they had been presented with their photographs in prior studies. These two locations represent different degrees of familiarity. Photographs of the Yerkes chimpanzees had been used in studies of face processing since the mid 1990s and, while it is difficult to quantify exactly how many times each individual had been shown over the course of the 15-year testing history, these individuals were considered to be highly familiarized. Moreover, in our previous studies, these photographs have been primarily frontal orientations, with only small

deviations in viewpoint being used. In contrast, photographs of the chimpanzees from Bastrop had been used as stimuli since 2004, and since this time the use of stimuli from both locations had been quantified, making it easier to assess the degree of familiarity subjects had with the individuals presented. Of the seven Yerkes chimpanzees included in this study, seven different photographs of four individuals, and five different photographs of three individuals had been shown in previous experiments. Of the eight Bastrop chimpanzees included in this study, two different photographs of two individuals, and 3, 4, 5, 7, 8, and 12 different photographs of the remaining six individuals had been shown previously. Each photograph showed a slightly different facial viewpoint, although most were within the frontal to 3/4 profile range as defined by the conditions of our research. Because this study used only novel photographs, the selection of each individual, regardless of location, was dependent on the availability of the stimulus database containing several full-frontal photographs and at least one 3/4 view. Therefore, it was not possible to standardize the exact number of times each individual had been seen in previous studies.

Unfamiliar faces were also acquired from chimpanzees living at the MD Anderson Cancer Center research facility in Bastrop, TX. These individuals had never before been seen by the subjects in this study. Both full-frontal and different facial viewpoints were presented. The 3/4 profile images were rotated in-depth along the vertical axis with the head turned approximately 30° – 45° to the right or left. Both eyes were visible in all cases. These images are available upon request.

2.3 Procedures

Subjects were tested with computerized-joystick MTS tasks. According to the MTS procedure, subjects are first shown a single image on the computer monitor, referred to as the sample, or the image to match. For the purposes of this experiment, the sample was always a frontally oriented face. 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, two additional images appeared simultaneously on the screen, equidistant from the sample on the opposite side of the monitor. One image matched the sample (target) in that it showed the same individual, either the exact same photograph or a different viewpoint of the sample individual. The non-matching image (foil) was a different individual than the one presented in the sample. Figure 1 illustrates the two types of MTS trials used in these experiments; full-frontal and 3/4-viewpoint trials.

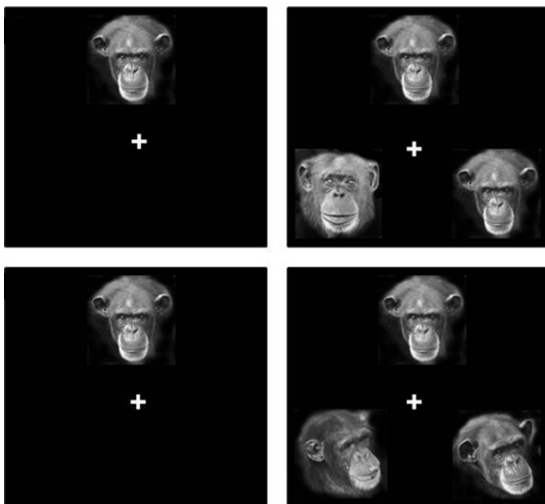


Figure 1. An example of the two types of matching trials: (a) full-frontal control trial and (b) a 3/4-viewpoint trial.

A correct response to the target was followed by a small food reward (squirt juice) and an inter-trial interval (ITI) of 2 s, while an incorrect response to the foil was followed by an ITI of 6 s and no food reinforcement. The next trial was then presented.

2.4 Familiar-face task

In the familiar-face task, subjects were presented with 30 unique trials, 15 showing full-frontal faces and 15 showing 3/4-viewpoint faces, faces rotated in-depth 30°–45°. The 15 full-frontal trials were considered control trials because the sample and target stimuli were identical images, while the foils showed a full-frontal face of a different chimpanzee. Each of the 15 trials showed novel chimpanzees, so photographs of 30 different individuals were required for these trials. The other 15 trials were 3/4-viewpoint trials. These trials contained the exact same sample images as presented in the full-frontal trials, but the correct choice was now a different facial viewpoint of the sample individual (see description above, figure 1). The foil individuals differed in identity from those presented in the full-frontal trials and these showed facial viewpoints that matched approximately the orientation of the target.

Although subjects had seen pictures of the individuals used in the familiar-face task in previous studies, the present studies used novel photographs: they had never been used in previous experiments. To ensure their familiarity, we first trained subjects to discriminate the full-frontal trials until their performance exceeded 85%. In each testing session, subjects received 4 repetitions of each trial, so daily testing sessions consisted of 60 trials. After reaching this criterion, the 15 3/4-viewpoint trials were added and subjects received 4 sessions of the combined 30 trials, in which 2 repetitions of each trial were presented per day (60 trials). Data analyses then compared performance on the 120 full-frontal control trials and 120 3/4-viewpoint trials.

2.5 Novel-face task

In the novel-face task, subjects were again presented with 30 trials, 15 full-frontal and 15 3/4-viewpoint trials. All of the individuals shown in the novel-face task depicted chimpanzees that the subjects had never seen before. The format for the novel-face trials was the same as that of the familiar-face trials. The 15 full-frontal trials showed the same stimuli as sample and targets, with a different individual as the foil. The 3/4-viewpoint trials presented exactly the same 15 full-frontal sample stimuli, but the target now showed a different facial viewpoint of this individual. Additionally, the foil individuals were different chimpanzees from those presented as foils in the full-frontal task, matched to the facial viewpoint of the targets. Unlike the familiar-face task, no initial training was given on any of the trials, full-frontal or 3/4-viewpoint. Subjects were presented with the combined 30 trials and tested in 4 sessions in which they received 2 repetitions per session, totaling 120 control and 120 3/4-viewpoint trials.

2.6 Data analysis

A repeated-measures ANOVA was performed in which there were two within-subject variables: view (full-frontal versus 3/4-viewpoint) and familiarity (familiar versus novel). Follow-up comparisons were performed where appropriate using *t*-tests. α was set at $p < 0.05$. Bonferroni's correction was used to adjust α for multiple comparisons made in the follow-up tests, where appropriate.

3 Results

Figure 2 shows the mean performance of subjects on each of the four stimulus categories. A 2×2 repeated-measures ANOVA revealed significant main effects of viewpoint ($F_{1,5} = 27.65$, $p < 0.003$) and familiarity ($F_{1,5} = 34.54$, $p < 0.002$), and a significant interaction between viewpoint and familiarity ($F_{1,5} = 7.47$, $p < 0.05$). Subjects performed significantly better matching the full-frontal (mean = 85.04%, SEM = 2.74%) compared

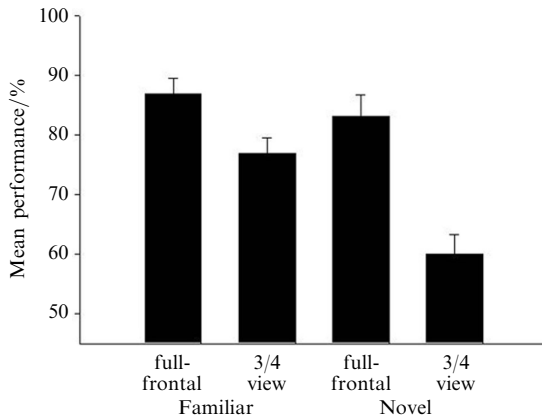


Figure 2. Mean (+SEM) performance matching familiar and novel faces in frontal orientation and across a change in viewpoint.

to 3/4-viewpoint trials (mean = 68.40%, SEM = 2.66%), and familiar (mean = 81.88%, SEM = 2.16%) compared to unfamiliar stimuli (mean = 71.57%, SEM = 2.53%). To follow-up on the significant interaction between viewpoint and familiarity, four paired t -tests were performed. Bonferroni's correction was applied making the level for significance $p < 0.0125$. Performance on the novel faces was significantly better in the full-frontal orientation compared to 3/4-viewpoint, indicating a significant cost of changing view ($t_5 = 4.87$, $p < 0.005$). Subjects also performed significantly better matching familiar compared to novel faces in their rotated view ($t_5 = 5.79$, $p < 0.002$). No significant differences were observed matching the full-frontal trials regardless of familiarity ($t_5 = 1.26$, $p = 0.26$). Frontal images of unfamiliar individuals were not more difficult to discriminate than frontal images of familiar individuals. No significant difference was observed in matching familiar faces across a change in viewpoint, although this was very close to reaching the adjusted level of significance ($t_5 = 3.42$, $p = 0.019$), suggesting a modest cost of changing viewpoint.

To further analyze the effect of familiarity on viewpoint change, in a follow-up analysis we examined subjects' performance on only the familiar stimuli used during the test phase (combined control and 3/4-viewpoint trials). This was important to evaluate whether the results reported above were driven by viewpoint costs for only the highly familiar Yerkes' chimpanzees, compared to the Bastrop chimpanzees. A repeated-measures ANOVA was conducted using colon location (Yerkes versus Bastrop) and viewpoint (frontal/control versus 3/4-view) as the within-subject variables. Significant main effects were found for both location ($F_{1,5} = 6.61$, $p = 0.05$) and viewpoint ($F_{1,5} = 11.16$, $p < 0.03$). Subjects performed better on the more familiar Yerkes chimpanzees' faces (mean = 83.93%, SEM = 2.43%) compared to the Bastrop chimpanzees (mean = 80.08%, SEM = 2.16%) and, as reported above, performance was better for the frontal/control

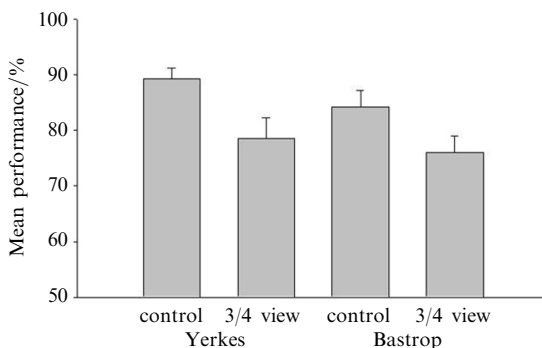


Figure 3. Mean (+SEM) performance matching familiar faces in their frontal orientation and across a change in viewpoint.

faces than the 3/4-view faces. There was, however, no significant interaction between location and viewpoint ($F_{1,5} = 0.28$, $p = 0.62$)—see figure 3). Therefore, a performance cost for matching faces after a 3/4-viewpoint change was present when the faces from both colonies were used.

4 General discussion

In this study we examined the effect of familiarity on the ability of chimpanzees to match faces across a change in viewpoint. Subjects were presented with full-frontal faces and faces rotated in-depth approximately 30° to 45° , ie 3/4 view. The photographs included both familiar chimpanzees, individuals whose faces had become familiarized both through subjects' prior testing history, and a pre-test training phase, and unfamiliar chimpanzees that the subjects of this study had never seen before. Notably, all of the photographs presented in this study were novel to ensure that performance was not affected by prior reinforcement history with specific pictorial stimuli (Burton et al 2005). Overall, subjects performed better matching the familiar compared to novel individuals' faces, and for the full-frontal compared to the 3/4-viewpoint faces. Importantly, subjects' performance was significantly impaired only when the novel faces were presented across a change in viewpoint. This could not be explained simply by the main effect of familiarity, mentioned above, as there was no significant difference between matching the familiar and novel faces when presented in their full-frontal orientation. The ability of chimpanzees to easily match frontally oriented unfamiliar faces is consistent with our previous findings (Parr et al 2000, 2010). Therefore, similar to humans, these results suggest that the ability of chimpanzees to recognize individual identity across a change in viewpoint is aided by familiarity (Hill and Bruce 1996; Troje and Kersten 1999).

Unlike in-plane rotations, where the upright face is the most canonical view and recognition decreases linearly as faces are rotated from upright to inverted (Collishaw and Hole 2002), it is unclear whether faces rotated in-depth have a canonical view. Human studies with unfamiliar faces reported that the 3/4-view was the most accurate for recognition, suggesting that it may be the most diagnostic (Bruce et al 1987; Hill et al 1997; Krouse 1981; Logie et al 1987). A prevailing view of human face processing is that identity is extracted through holistic processing which functions to integrate features into a single perceptual whole (Rossion 2008; Tanaka and Farah 1993). A 3/4-view may be the best view for extracting information about features on both sides of the face, in addition to emphasizing important surface-based cues, such as shading, that may be more difficult to garner from frontal orientations (Bruce and Langton 1994; Hill and Bruce 1996). Others have confirmed that in the ability to extract information from facial features unaffected by a shift from full-frontal to 3/4-views the eyes were most important, and nose and mouth together were more important than either individually (Stephan and Caine 2007). Previous studies in our lab have shown that chimpanzees utilize holistic processing when discriminating conspecifics' faces (Parr et al 2006; Taubert et al, submitted), and numerous studies have demonstrated their sensitivity to in-plan rotations (Parr et al 1998, 2006). Although holistic processing and the use of configural cues has been shown to be relatively stable across changes in viewpoint, profile views were the most difficult to recognize (McKone 2008). One exception to this is when faces are highly distinctive. Regardless of familiarity, the recognition of distinctive faces is more impervious to changes in viewpoint than that of typical faces common in everyday encounters (Newell et al 1999).

How does familiarity affect the ability to recognize faces across a change in viewpoint? Previous studies in non-human primates, using both electrophysiological recordings and functional neuroimaging, have identified populations of cells in superior temporal sulcus that respond in both a viewpoint-dependent and viewpoint-independent manner (De Souza et al 2005; Perrett et al 1985, 1991; Rolls et al 1989; Tsao et al 2006). Drawing from these

findings, Jeffery et al (2007) proposed that familiarity may increase the connections among view-specific neurons such that familiar faces are coded with greater view-invariance than unfamiliar faces. Human studies using fMRI have shown adaptation of BOLD responses in the FFA to the presentation of familiar, but not unfamiliar, faces presented across different viewpoints. The lack of adaptation suggests that different views of the same unfamiliar face were processed in a manner similar to different individuals' faces (Andrews and Ewbank 2004). Other studies report that damage to regions of the medial temporal lobe, perirhinal cortex, selectively impairs the ability to discriminate faces across different viewpoints, but not when the same viewpoint was used (Buckley et al 2001). Among healthy adults, this region shows greater activity when faces and objects are presented across a change in viewpoint (Barense et al 2010). This suggests that the ability to recognize faces across a viewpoint change relies on more than just perceptual matching, but recruits memory processes as well. This is consistent with previous suggestions that the difference between familiar- and unfamiliar-face processing goes beyond simple quantitative differences. Burton et al (2005), for example, proposed that familiarity increases the ability of people to ignore the irrelevant pictorial information present in photographs and concentrate on information that is diagnostic of identity. In unfamiliar faces, it is not clear what information is diagnostic and what is a spurious byproduct of photographic stimuli. Therefore, when familiar faces are encountered in atypical or partly occluded conditions, holistic and configural processing strategies function to access stored representations of those features and match them to the current view. This would not be possible for unfamiliar faces, as there would be no information available on how to complete the face.

There are several limitations to this study. First, we only presented one change in viewpoint, the 3/4 view. Therefore, it is unclear in chimpanzees how deviant the view must be to significantly impair the discrimination of faces. In humans, researchers have demonstrated that the recognition of unfamiliar synthetic faces could be affected by in-depth rotations of as little as 13° – 20° and many studies described above suggest that the 3/4-view may be the most diagnostic, while the profile view may be the most difficult to recognize (Lee et al 2006). Further studies are needed to determine if these same findings would be supported in chimpanzees. Although familiarity conferred an advantage to chimpanzees when discriminating faces across a change in viewpoint, these faces had additionally been familiarized in their frontal orientation prior to the 3/4-viewpoint change. Analysis of performance in matching only the familiar faces showed that subjects were better for the more familiar Yerkes compared to Bastrop chimpanzees. Because the unfamiliar faces were not similarly familiarized, we are also unable to disentangle whether familiarity alone or familiarity across a range of viewpoints is the more important source of information for viewpoint-independence to emerge (see Troje and Kersten 1999). Because the chimpanzees performed as well in matching the familiar and novel faces in their frontal orientation, we believe that experience with faces across a range of viewpoints is more important than familiarity, per se, although this remains to be tested. Finally, this study was possible because the faces of numerous conspecifics had become familiarized over many years of prior research. Although the requirements of this study made it impossible to select stimuli that had equivalent exposure histories, our follow-up analyses showed that performance costs after a change in viewpoint was similar regardless of whether the faces had been familiarized over 15 years of study (Yerkes), or seen in only a handful of photographs (Bastrop). These results suggest that performance advantages for discriminating familiar faces across a change in viewpoint can appear quickly. Thus, we propose that familiarization is a robust mechanism for strengthening the representation of faces and has been conserved in primates to achieve efficient individual recognition over a range of natural viewing conditions.

Acknowledgments. This investigation was supported by RR-00165 from the NIH/NCRR to the Yerkes National Primate Research Center, and R01-MH068791 to L A Parr. The Yerkes National Primate Research Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care. Thanks to Daniel Brubaker and Kim Weldon for assistance with animal testing and the animal care staff at the Yerkes National Primate Research Center. Special thanks to Steve Shapiro and Susan Pavonetti and the MD Anderson Cancer Center, Bastrop, TX for help in acquiring photographs of unfamiliar chimpanzees.

References

- Andrews T J, Ewbank M P, 2004 “Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe” *NeuroImage* **23** 905–913
- Barense M D, Henson R N A, Lee A C H, Graham K S, 2010 “Medial temporal lobe activity during complex discrimination of faces, objects, and scenes: Effect of viewpoint” *Hippocampus* **20** 389–401
- Biederman I, 1987 “Recognition-by-components: A theory of human image understanding” *Psychology Review* **94** 115–147
- Bruce V, 1982 “Changing faces: Visual and non-visual coding processes in face recognition” *British Journal of Psychology* **73** 105–116
- Bruce V, Langton S, 1994 “The use of pigmentation and shading information in recognizing the sex and identities of faces” *Perception* **23** 803–822
- Bruce V, Valentine T, Baddeley A, 1987 “The basis of the 3/4 view advantage in face recognition” *Applied Cognitive Psychology* **1** 109–120
- Buckley M J, Booth M C, Rolls E T, Gaffan D, 2001 “Selective perceptual impairments after perirhinal cortex ablation” *Journal of Neuroscience* **21** 9824–9836
- Bülthoff H H, Edelman S, 1992 “Psychophysical support for a two-dimensional view interpolation theory of object recognition” *Proceedings of the National Academy of Sciences of the USA* **89** 60–64
- Burton A M, Jenkins R, Hancock P J B, White D, 2005 “Robust representations for face recognition: The power of averages” *Cognitive Psychology* **51** 256–284
- Collishaw S M, Hole G J, 2002 “Is there a linear or a nonlinear relationship between rotation and configural processing of faces?” *Perception* **31** 287–296
- De Souza W C, Eifuku S, Tamura R, Nishijo H, Ono T, 2005 “Differential characteristics of face neuron responses within the anterior superior temporal sulcus of macaques” *Journal of Physiology* **94** 1252–1266
- Diamond R, Carey S, 1986 “Why faces are and are not special: An effect of expertise” *Journal of Experimental Psychology* **115** 107–117
- Favelle S K, Palmisano S M, Maloney R T, 2007 “Things are looking up: Differential decline in face recognition following pitch and yaw rotations” *Perception* **36** 1334–1352
- Gothard K M, Brooks K N, Peterson M A, 2009 “Multiple perceptual strategies used by macaque monkeys for face recognition” *Animal Cognition* **12** 155–167
- Hancock P J B, Bruce V, Burton A M, 2000 “Recognition of unfamiliar faces” *Trends in Cognitive Sciences* **4** 330–337
- Hill H, Bruce V, 1996 “Effects of lighting on the perception of facial surfaces” *Journal of Experimental Psychology: Human Perception and Performance* **22** 986–1004
- Hill H, Schyns P G, Akamatsu S, 1997 “Information and viewpoint dependence in face recognition” *Cognition* **62** 201–222
- Jeffery L, Rhodes G, Busey T, 2007 “Broadly tuned, view-specific coding of face shape: Opposing figural aftereffects can be induced in different views” *Vision Research* **47** 3070–3077
- Johnston R A, Edmonds A J, 2009 “Familiar and unfamiliar face recognition: A review” *Memory* **17** 577–596
- Krouse F L, 1981 “Effects of pose, pose change, and delay on face recognition performance” *Journal of Applied Psychology* **66** 651–654
- Lee Y, Matsumiya K, Wilson H R, 2006 “Size-invariant but viewpoint-dependent representation of faces” *Vision Research* **46** 1901–1910
- Logie R H, Baddeley A D, Woodhead M M, 1987 “Face recognition, pose and ecological validity” *Applied Cognitive Psychology* **1** 53–69
- McKone E, 2008 “Configural processing and face viewpoint” *Journal of Experimental Psychology: Human Perception and Performance* **34** 310–327
- Maurer D, Le Grand R, Mondloch C J, 2002 “The many faces of configural processing” *Trends in Cognitive Sciences* **6** 255–260
- Mervis C, Rosch E, 1981 “Categorization of natural objects” *Annual Review of Psychology* **32** 89–115

- Newell F N, Chiroro P, Valentine T, 1999 "Recognizing unfamiliar faces: The effects of distinctiveness and view" *Quarterly Journal of Experimental Psychology A* **52** 509–534
- Parr L A, 2011 "The evolution of face processing in primates" *Philosophical Transactions of the Royal Society of London B* **366** 1764–1777
- Parr L A, Dove T, Hopkins W D, 1998 "Why faces may be special: Evidence for the inversion effect in chimpanzees (*Pan troglodytes*)" *Journal of Cognitive Neuroscience* **10** 615–622
- Parr L A, Heintz M, Akamagwuna U, 2006 "Three studies of configural face processing by chimpanzees" *Brain and Cognition* **62** 30–42
- Parr L A, Heintz M, Lonsdorf E, Wroblewski E, 2010 "Visual kin recognition in nonhuman primates: Inbreeding avoidance or male distinctiveness" *Journal of Comparative Psychology* **124** 343–350
- Parr L A, Winslow J T, Hopkins W D, de Waal F B M, 2000 "Recognizing facial cues: Individual recognition in chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*)" *Journal of Comparative Psychology* **114** 47–60
- Perrett D I, Oram M W, Harries M H, Bevan R, Hietanen J K, Benson P J, Thomas S, 1991 "Viewer-centred and object-centred coding of heads in the macaque temporal cortex" *Experimental Brain Research* **86** 159–173
- Perrett D I, Smith P A J, Potter D D, Mistlin A J, Head A S, Milner A D, 1985 "Visual cells in the temporal cortex sensitive to face view and gaze direction" *Proceedings of the Royal Society of London, Series B* **223** 293–317
- Poggio T, Edelman S, 1990 "A network that learns to recognize three-dimensional objects" *Nature* **343** 263–266
- Pokorny J J, de Waal F B M, 2009 "Face recognition in capuchin monkeys (*Cebus apella*)" *Journal of Comparative Psychology* **123** 151–160
- Rolls E T, Baylis G C, Hasselmo M E, Nalwa V, 1989 "The effect of learning on the face selective responses of neurons in the cortex in the superior temporal sulcus of the monkey" *Experimental Brain Research* **76** 153–164
- Rosenfeld S A, Van Hoesen G W, 1979 "Face recognition in the rhesus monkey" *Neuropsychologia* **17** 503–509
- Rossion B, 2008 "Picture plane inversion leads to qualitative changes in face perception" *Acta Psychologica* **128** 274–289
- Stephan B C M, Caine D, 2007 "What is in a view? The role of featural information in the recognition of unfamiliar faces across viewpoint transformation" *Perception* **36** 189–198
- Tarr M J, Pinker S, 1989 "Mental rotation and orientation-dependence in shape recognition" *Cognitive Psychology* **21** 233–282
- Tanaka J W, Farah M J, 1993 "Parts and whole in face recognition" *Quarterly Journal of Experimental Psychology A* **46** 225–245
- Taubert J, Marsh P J, Shaw T, 2010 "When you turn the other cheek: A preference for novel viewpoints of familiar faces" *Perception* **39** 429–432
- Taubert J, Qureshi A A, Parr L A, submitted, "The composite effect in chimpanzees and monkeys"
- Troje N F, Kersten D, 1999 "Viewpoint-dependent recognition of familiar faces" *Perception* **28** 483–487
- Tsao D Y, Freiwald W A, Tootell R B H, Livingstone M S, 2006 "A cortical region consisting entirely of face-selective cells" *Science* **311** 670–674
- Valentine T, 1988 "Upside-down faces: a review of the effects of inversion upon face recognition" *British Journal of Psychology* **79** 471–491
- Yin R K, 1969 "Looking at upside-down faces" *Journal of Experimental Psychology* **81** 141–145

ISSN 0301-0066 (print)

ISSN 1468-4233 (electronic)

PERCEPTION

VOLUME 40 2011

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