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Original Article

Cues to Personality and Health in the Facial Appearance of Chimpanzees (*Pan troglodytes*)

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Abstract: Humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*) can extract socially-relevant information from the static, non-expressive faces of conspecifics. In humans, the face is a valid signal of both personality and health. Recent evidence shows that, like humans, chimpanzee faces also contain personality information, and that humans can accurately judge aspects of chimpanzee personality relating to extraversion from the face alone (Kramer, King, and Ward, 2011). These findings suggest the hypothesis that humans and chimpanzees share a system of personality and facial morphology for signaling socially-relevant traits from the face. We sought to test this hypothesis using a new group of chimpanzees. In two studies, we found that chimpanzee faces contained health information, as well as information of characteristics relating to extraversion, emotional stability, and agreeableness, using average judgments from pairs of individual photographs. In a third study, information relating to extraversion and health was also present in composite images of individual chimpanzees. We therefore replicate and extend previous findings using a new group of chimpanzees and demonstrate two methods for minimizing the variability associated with individual photographs. Our findings support the hypothesis that chimpanzees and humans share a personality signaling system.

Keywords: chimpanzee, personality, health, face, signal

Introduction

Humans can detect personality and other socially-relevant information from the static, non-expressive faces of strangers. In much the same way that transient emotional states can be communicated through facial expression, more stable predispositions to behavior can be communicated through more stable facial structure. That is, people with similar personalities can have similar-looking faces. Human faces provide accurate information with regard to many socially-relevant traits, including “Big Five” personality

traits (Kramer and Ward, 2010; Little and Perrett, 2007), health (Kramer and Ward, 2010), sexual strategies (Boothroyd, Jones, Burt, DeBruine, and Perrett, 2008), trustworthiness (Stirrat and Perrett, 2010), aggression (Carré, McCormick, and Mondloch, 2009), and dominance (Mueller and Mazur, 1997). Such findings demonstrate that human facial morphology contains information associated with stable patterns of behavior, and that other humans can identify and use this information. Although there is a growing literature on emotional expression in humans, chimpanzees, and other primates (e.g., Parr, 2003), it is unknown whether non-human primates may demonstrate similar associations between facial appearance and personality. Here we investigate the possibility that chimpanzees may have facial cues to personality that conspecifics can use. We do so by examining a necessary but not sufficient requirement: is chimpanzee facial appearance associated with specific personality characteristics?

The possibility that chimpanzees, like humans, may express and recognize personality on the face seems plausible for at least two reasons. First, chimpanzees have stable personality structures. We know that nonhuman species can demonstrate stable, context-general behavioral biases (for reviews, see Gosling and John, 1999; Mehta and Gosling, 2008). Analyses of chimpanzee personality produced a structure similar to that of humans (King and Figueiredo, 1997). In addition to five factors demonstrating remarkable overlap with the human model, a dominance-related factor was also discovered in chimpanzees that showed high heritability (Weiss, King, and Figueiredo, 2000), along with both reliability (Freeman and Gosling, 2010) and validity in predicting individual, real-world behaviors (Pederson, King, and Landau, 2005).

Second, while we do not know if chimpanzees can recognize personality in others, it is clear that the face is an important social stimulus. Chimpanzees and other nonhuman primates extract a range of socially-relevant information from the face for social purposes. Facial information can be used for individual discrimination of conspecifics (Dufour, Pascalis, and Petit, 2006; Parr, Winslow, Hopkins, and de Waal, 2000). Faces can also be used to discriminate males from females (e.g., Japanese macaques: Koba, Izumi, and Nakamura, 2009), and in-group from out-group members (e.g., capuchin monkeys: Pokorny and de Waal, 2009). Indeed, chimpanzees are able to use facial information from unfamiliar conspecifics to determine relatedness (Parr and de Waal, 1999; Parr, Heintz, Lonsdorf, and Wroblewski, 2010), and rhesus macaque faces also contain kinship information (Bower, Suomi, and Paukner, 2011). Recently, research has shown that socially-relevant information relating to dominance and rank is present in the faces of nonhuman primates (e.g., mandrills: Setchell and Wickings, 2005; drills: Marty, Higham, Gadsby, and Ross, 2009), and that facial information can be used by others to discriminate individuals based on social status (e.g., rhesus macaques: Deaner, Khera, and Platt, 2005).

It would be important to know if chimpanzee faces did contain cues to personality because this would suggest a previously unknown form of social information that was available to others. This system would require, first, that personality information is expressed on the face of chimpanzees; and second, that this information is recognized and used by conspecifics. We therefore carried out three experiments to test the first of these requirements, i.e., to determine whether chimpanzee faces carry information about the chimpanzees' stable personality traits. While evidence of this would not testify to the use of

this information by chimpanzees, it remains a necessary step in establishing the presence of such a system.

Previous results suggest that individual personality information is indeed available within the chimpanzee face because human judges were able to accurately identify certain aspects of personality from static, non-expressive photographs (Kramer, King, and Ward, 2011). Specifically, untrained humans were able to accurately perceive personality characteristics relating to extraversion—in particular, how dominant an individual was, from individual photographs of non-expressive chimpanzee faces.

It is important to understand exactly what we mean by ‘accurate perceptions’ of chimpanzee personality. Given that self-report methods cannot be used with animals, researchers are forced to use human observers in order to assess animal personality. With humans, there is evidence that ratings provided by others, well-acquainted with the target individuals, produce reliable, stable, and valid assessments of personality (e.g., Funder, Kolar, and Blackman, 1995; Riemann, Angleitner, and Strelau, 1997). A frequent approach when assessing non-human animals including chimpanzees is to collect ratings from keepers or others who are well-acquainted with the target individuals (e.g., King and Figueredo, 1997).

Chimpanzee trait ratings provided by humans have demonstrated strong convergent correlations with behavioral coding methods, as well as showing greater reliability than behavioral coding (Vazire, Gosling, Dickey, and Schapiro, 2007). In addition to high levels of interobserver consensus (Gosling, 2001; Gosling and Vazire, 2002), trait ratings have been validated against real-world behaviors and outcomes with many non-human primates (e.g., rhesus monkeys: Capitanio, 1999; Stevenson-Hinde, Stillwell-Barnes, and Zunz, 1980; and vervet monkeys: McGuire, Raleigh, and Pollack, 1994), and in particular, with chimpanzees (Murray, 2011; Pederson et al., 2005; Uher and Asendorpf, 2008). For example, ratings of aggressiveness and timidity showed correlations in the expected directions with dominance rank in wild chimpanzees (Buirski, Plutchik, and Kellerman, 1978). In addition, ratings of trait psychopathy correlated with specific behaviors in research centre chimpanzees, and these behaviors were similar to those seen in human psychopaths (Lilienfeld, Gershon, Duke, Marino, and de Waal, 1999). Primate personality has also shown relationships with underlying hormonal and other biological factors (Anestis, Bribiescas, and Hasselschwert, 2006; Champoux, Higley, and Suomi, 1997; Maninger, Capitanio, Mendoza, and Mason, 2003; Sapolsky, 1999). As such, ratings data have been consistently shown to be a useful, valid, and readily collectable measure of personality for non-human primates in general, and chimpanzees more specifically (Gosling, 2001).

Further, chimpanzee personality as measured with trait ratings shows stability across time (Dutton, 2008), and differences relating to age and sex that are comparable to those found in humans (King, Weiss, and Sisco, 2008). Personality measures as assessed by trait ratings have also demonstrated heritability of chimpanzee personality factors (e.g., dominance: Weiss et al., 2000; and subjective well-being: Weiss, King, and Enns, 2002). Therefore, a growing body of research has shown that chimpanzee trait ratings are measuring broad and stable behavioral biases (Vazire et al., 2007; also see Freeman and Gosling, 2010, for a review). As such, we consider trait ratings provided by people familiar

with the individual chimpanzees as a measure of actual personality profiles, and compare these with naive judges' perceptions in order to produce a measure of accuracy. In the current experiments, we therefore follow previous methods (Kramer et al., 2011) by using trait ratings from zoo keepers highly familiar with the behaviors of the animals within the group to provide "actual" personality ratings.

Given the importance of findings demonstrating personality information in the chimpanzee face, the current research aims to replicate the one previous finding of facial cues to dominance (Kramer et al., 2011) using a new group of chimpanzees. This previous research relied on a single image of each chimpanzee that was not collected with stimulus presentation in mind. Here, we collected more controlled photographic stimuli, allowing us to present multiple images of each individual (as well as average images) in order to better address possible issues with idiosyncrasies of picture lighting, viewpoint, and other irrelevant factors. Finally, we were able to collect health information regarding this chimpanzee group. Previous studies with chimpanzees have found an association between health and fluctuating asymmetry in the face (Sefcek and King, 2007). However, we have seen that in humans there are cues within the static face that predict health (Kramer and Ward, 2010), which are not due to fluctuating asymmetry. Here, we further examine the extent to which there are valid cues for health which can be identified across species.

Study 1a: Accurate personality identification from the chimpanzee face

The first experiment served to replicate previous findings with a new chimpanzee group using a ratings methodology. There were two parts to our general method. First, we collected photographs and personality characteristics for the twelve members of a chimpanzee group living at the Welsh Mountain Zoo in Colwyn Bay. Second, we asked untrained observers to rate the personality characteristics of the chimpanzees solely on the basis of these photos. Based on previous findings, we expected that the observers would show above-chance accuracy on characteristics related to extraversion, and possibly other traits as well.

Methods – Chimpanzee personalities and photographs

Here we describe the procedures used to generate the chimpanzee photographs and personality ratings. Previous studies used photographs which were not created with the intention of a front-facing neutral expression. Collecting our own photographic stimuli provided more control and higher quality, and the use of two photographs for each individual helped us to avoid any idiosyncrasies in judgments due to specific photographs. Personality measures were based on a group of six keepers who were highly familiar with the animals.

Chimpanzees

The group comprised 12 chimpanzees (6 males) living at the Welsh Mountain Zoo (Colwyn Bay, UK). Ages ranged from 8 to 44 years ($M = 21.75$, $SD = 10.07$) and almost exclusively comprised adults. This group of chimpanzees has not appeared in previous

research and so their profiles are summarized in Table 1.

Table 1. A summary of the Welsh Mountain Zoo chimpanzee group.

Name	Sex	Age during collection	Birth place	Age on arrival at zoo
Mabel	Female	44	Wild	approx. 5
Sixpence	Male	30	WMZ	0
Katie	Female	28	Belfast Zoo	6
Groat	Male	26	WMZ	0
Coron	Male	24	WMZ	0
Tuppence	Female	23	Chester Zoo	2 months
Bob*	Male	21	WMZ	0
Jill	Female	21	Belfast Zoo	7
Nickel	Male	15	WMZ	0
Jessie	Female	11	WMZ	0
Jasper	Male	10	WMZ	0
Euro	Female	8	WMZ	0

Note. Ages are in years unless otherwise specified. WMZ = Welsh Mountain Zoo.

* This chimpanzee died in July 2011.

Personality ratings

Personality and health ratings were made by six zoo employees who had extensive experience with the chimpanzees (years of experience $M = 6.58$, $SD = 3.83$). By averaging ratings from multiple observers, we minimized individual idiosyncrasies, including potential errors in perception and personal biases. All six raters completed ratings for every chimpanzee and interrater reliability was calculated.

Ratings were completed using a 52-item extended version of the Chimpanzee Personality Questionnaire (CPQ; King and Figueredo, 1997). The original version of this questionnaire (King and Figueredo, 1997) demonstrated a six-factor chimpanzee personality structure that was largely consistent across different settings (Weiss, King, and Hopkins, 2007; Weiss et al., 2009), showed high heritability of trait dominance (Weiss et al., 2000), found differences relating to age and sex that are comparable to those found in humans (King et al., 2008), and predicted the occurrence of real-world behaviors (Pederson et al., 2005). In the current version, three adjectives (i.e., clumsy, autistic, manipulative) were deleted in line with previous results (King and Figueredo, 1997), while twelve additional adjectives were included. These comprised curious, thoughtless, individualistic,

distractible, vulnerable, innovative, cool, unperceptive, conventional, quitting, anxious, and healthy. All items were followed by one to three sentences that defined the adjective within the context of chimpanzee behavior and were consistent with dictionary definitions. For example, “Dominant: Subject is able to displace, threaten, or take food from others. Or subject may express high status by decisively intervening in social interactions”.

Each adjective was rated on a seven-point Likert scale (1 = “Displays either total absence or negligible amounts of the trait”; 7 = “Displays extremely large amounts of the trait”), and raters were instructed to base their judgments on overall impressions and not estimated frequencies of particular behaviors. Average ratings were produced for each adjective. There were three cases in which a questionnaire item was not completed. In these cases, average ratings for that adjective were calculated from the remaining five zoo employees’ ratings. Raters were also instructed not to discuss their ratings with other raters.

Interrater reliability was calculated for each adjective using Cronbach’s α , using the six ratings for each of the 12 chimpanzees. Cronbach’s α values ($M = 0.59$, $SD = 0.24$) formed a continuous distribution ranging from -0.01 (*distractible*) to 0.91 (*playful*) for the 52 items. Alpha values for the specific traits we tested are given in the methods sections below, and were comparable with equivalent findings in the human and animal personality literatures (Funder et al., 1995; Gosling, 2001).

Photographs

Multiple photographs were taken of each of the 12 chimpanzees at the zoo over a five-week period using a digital camera and zoom lens. Of these photographs, the two highest quality images were selected for each individual in which the chimpanzees were looking towards the camera. Views of the faces in these photographs ranged from straight-on to three-quarter view. Images were chosen without valenced facial expressions (e.g., with closed mouths and without strong shadowing over the eyes). These images were cropped to show only the head, with a small amount of neck/body and background remaining (see Figure 1). Images were approximately 275 x 300 pixels in size, and about 7 x 7.5cm on the screen.

Figure 1. The two individual images of Groat used in Study 1 (left and center), and the prototype image used in Study 2 (right).



Methods – Experimental judgments

In this part of the study, we presented the chimpanzee images to untrained observers, to be rated on a variety of personality characteristics.

Participants

Thirty-six students from Bangor University (age range, 18-39 years; 27 females) took part in this study in exchange for course credits.

Stimuli

The 24 images described above, two for each chimpanzee, were used.

Procedure

Participants were shown the images on the computer screen one at a time and instructed to rate them on a scale of 1 (very low) to 7 (very high). The stimuli were rated on six characteristics (Cronbach's α of zoo employee ratings in brackets): dominant (0.82), active (0.83), sympathetic (0.57), healthy (0.89), sociable (0.64), and fearful (0.75). This selection was motivated by previous findings suggesting accuracy with the first three of these characteristics, along with significant inaccuracy with 'sociable' (Kramer et al., 2011). 'Fearful' was chosen for its high interrater reliability and high loading on the chimpanzee trait of Dominance, and 'healthy' was included as this has not yet been investigated with chimpanzee faces. A description of each characteristic, taken from the CPQ used during stimulus creation, appeared onscreen while that rating was being made. The characteristics were blocked separately, and the order of block presentation was counterbalanced between participants. Trials appeared in randomized order for each participant.

Results and Discussion

For each participant, we calculated the adjective rating for each chimpanzee by averaging the ratings of the two images of that individual. Rater consensus for each adjective can be found in Table 2. Individual accuracy was calculated as in Back et al. (2010), by correlating these adjective ratings with the chimpanzees' personalities (mean zoo employee ratings) for each participant. These individual accuracies were then averaged across participants using Fisher's r -to- z transformation (which corrects the skew in the distribution of r) and are summarized in Table 2.

Table 2. Rater consensus and individual accuracy (Study 1a).

Trait	Individual Accuracy		
	Rater Consensus	Mean	Standard Deviation
Dominant	.98	0.28***	0.19
Active	.95	0.30***	0.42
Sympathetic	.98	0.07*	0.21
Healthy	.97	0.59***	0.33
Sociable	.98	0.32***	0.23
Fearful	.85	0.11*	0.29

Note. Consensus was calculated using Cronbach's α . Individual accuracies represent the average within-rater correlation between ratings and chimpanzee personalities.

*significantly different from zero at $p < .05$, *** $p < .0001$.

Significance testing was done using one-sample t tests, with participant as the unit of analysis (e.g., Back et al., 2010). Chance was defined as a mean individual accuracy of zero, which would indicate no relationship between the participants' ratings and the chimpanzees' personality profiles. As Table 2 shows, we found significant performance accuracy for dominant, active, and sociable. In addition, sympathetic and fearful were just significant.

These results demonstrate that characteristics relating to extraversion are accurately perceived in chimpanzee faces, replicating previous work in a completely different set of chimpanzees (Kramer et al., 2011). Kramer et al. found significant accuracy for 'dominant' and 'active', as well as results close to significant for 'sympathetic'. Interestingly, while 'sociable' was accurately judged in the current study, performance was significantly below chance in Kramer et al., who suggested that their results might reflect a bias on the part of human raters to assume that high dominance was not associated with high sociability. The current findings indicate that this is not necessarily the case. With this one exception, our findings largely replicate previous evidence of personality signals in the chimpanzee face, in a different set of chimpanzees and with a different set of keepers providing the chimpanzee personality profiles.

In addition, we found a highly significant correlation between participant ratings and profile measures of health, demonstrating signals of health in the chimpanzee face. We have previously seen that physical health associated with activities of daily living is signaled in the human face (Kramer and Ward, 2010). Previous studies have also shown that

fluctuating asymmetries (FA) in the chimpanzee face predict health (Sefcek and King, 2007), and FA may be a cue to health in our current results as well. However, we extend previous results by demonstrating that health information in the chimpanzee face can be accurately detected across species.

Study 1b: Investigating the role of age and gender perceptions

The second experiment investigated whether other characteristics could be accurately judged from the chimpanzee face. In addition, we explored how judgments of age and gender were related to ratings of dominance and other characteristics.

Methods

Participants

A different set of 41 students from Bangor University (age range, 18-42 years; 32 females) took part in this study in exchange for course credits.

Stimuli

The same images that were used in Study 1a.

Procedure

The procedure was identical to Study 1a. However, ratings were collected for these six characteristics (Cronbach's α of zoo employee ratings in brackets): dominant (0.82), healthy (0.89), solitary (0.69), independent (0.73), age, and gender. 'Solitary' and 'independent' were included as they load onto the traits Extraversion and Dominance respectively and may therefore also show accuracy in perceptions, following on from previous research (Kramer et al., 2011). Age was rated on a scale of 1 (very young) to 7 (very old), and gender was rated on a scale of 1 (very feminine) to 7 (very masculine). These characteristics were chosen to span several personality traits using only characteristics with relatively high zoo employee interrater agreement. As the main focus of the current research, 'dominant' and 'healthy' were included for a second time in order to investigate possible relationships with perceived age and gender. As before, a description of each characteristic appeared onscreen while that rating was being made.

Results and Discussion

Both rater consensus for each adjective and individual accuracy were calculated as in Study 1a, and the results are summarized in Table 3.

Table 3. Rater consensus, individual accuracy, and accuracy controlling for perceptions of age (Study 1b).

Trait	Individual Accuracy			Individual Accuracy Controlling For Age Perceptions	
	Rater Consensus	Mean	Standard Deviation	Mean	Standard Deviation
Dominant	.98	0.18***	0.22	0.17***	0.26
Healthy	.98	0.58***	0.24	0.42***	0.33
Solitary	.96	0.17***	0.24	0.16**	0.29
Independent	.96	0.19***	0.20	0.14**	0.27
Age	.98	0.46***	0.26	-	-

Note. Consensus was calculated using Cronbach's α . Individual accuracies represent the average within-rater correlation between ratings and chimpanzee profiles. These accuracies were also calculated using partial correlations, controlling for perceptions of age.

significantly different from zero at $p < .005$, * $p < .0001$.

By comparing participants' accuracy with chance, we found significant accuracy for dominant, healthy, solitary, independent, and age. Therefore, as well as various personality characteristics relating to extraversion and emotional stability, participants were accurately able to judge the ages of chimpanzees from the face alone. Age accuracy was not found in previous research (Kramer et al., 2011), and this may be explained by factors relating to the specific chimpanzee group used here. The number of members, and the variability of their ages, may have led to increased accuracy in the current study. However, our main concern was with how judgments of age were related to ratings of other traits.

We investigated how perceptions of age related to perceptions of personality and health. We found significant relationships between age ratings and perceptions of dominant, mean $z = .16$; $t(40) = 3.00$, $p = .0046$; healthy, mean $z = -.64$; $t(40) = 10.88$, $p < .0001$; masculinity, mean $z = .27$; $t(40) = 3.74$, $p = .0006$; solitary, mean $z = .51$; $t(40) = 8.51$, $p < .0001$; and independent, mean $z = .35$; $t(40) = 4.76$, $p < .0001$. Again, with four of these characteristics, an increase correlated with an increase in perceived age. In contrast, an increase in perceived health correlated with a decrease in ratings of age (i.e., younger looking chimpanzees were rated as healthier). The actual ages of the chimpanzees did not correlate significantly with any of these characteristics when considering the animals' personality profiles (all $ps > .07$). Therefore, although perceived age was strongly associated with other perceptions, such relationships were not present in the chimpanzee profiles.

Given that participants were accurate in judging age, we explored whether their perceptions of age could account for their accuracy on the other characteristics. Accuracy

was calculated as before, but using partial correlations controlling for perceptions of age (see Table 3). We again found significant performance accuracy for dominant, healthy, solitary, and independent. These results suggest that, although perceptions of age and other characteristics were related, participants' judgments of age did not fully account for their accurate performance.

We carried out similar analyses to investigate participants' ratings of gender. We calculated the mean gender rating for each chimpanzee by averaging the scores of all images of the individual. Male and female chimpanzees were not rated differently in terms of gender, $t(10) = 1.27$, $p = .23$, suggesting that participants were unable to tell the sex of the chimpanzees from their faces alone.

We also investigated how perceptions of gender related to perceptions of personality and health. We calculated the adjective rating for each chimpanzee by averaging the ratings of the two images of that individual. We then correlated these ratings with the gender ratings for each participant and applied Fisher's transformation. By comparing these correlations with chance, we found significant relationships between gender ratings and perceptions of dominant, mean $z = .66$; $t(40) = 14.30$, $p < .0001$; healthy, mean $z = -.23$; $t(40) = 4.97$, $p < .0001$; age, mean $z = .53$; $t(40) = 8.37$, $p < .0001$; solitary, mean $z = .57$; $t(40) = 7.63$, $p < .0001$; and independent, mean $z = .68$; $t(40) = 9.62$, $p < .0001$. With four of these characteristics, an increase correlated with an increase in perceived masculinity. In contrast, an increase in perceived health correlated with a decrease in ratings of masculinity (i.e., increased femininity). For the chimpanzee characteristics as rated by the zoo employees, males and females did not significantly differ in any of the comparisons above (all $p > .40$). Overall, it seems that untrained human raters were unable to identify chimpanzee sex from the face. While there were correlations between some gender and trait ratings, these correlations did not reflect actual sex differences as assessed by the zoo keepers.

Study 2: Dominance and health accuracy using average images

The third experiment served to investigate whether dominance and health traits could be accurately judged from composite images of chimpanzees. By using what are effectively prototypes created from averaging several photographs together for each individual, we addressed the issue of picture idiosyncrasies with a second methodology.

Methods

Participants

A different set of 30 students from Bangor University (age range, 18-48 years; 15 females) took part in this study in exchange for course credits.

Stimuli

A large set of photographs taken of the 12 chimpanzees formed our database, and these included both high and lower quality images, taken from different viewing angles. Only those without valenced facial expressions were used. All photographs used in Study 1

also appeared in the composites here. Multiple images of a single chimpanzee were averaged together using PsychoMorph software (Tiddeman, Burt, and Perrett, 2001), based on 126 key locations within the face and around the face outline, to produce a prototype image for that individual. The averaging together of multiple images of an individual has been shown to produce both an average pose and expression (Benson and Perrett, 1993), and improves recognition over single images (Burton, Jenkins, Hancock, and White, 2005; Jenkins and Burton, 2011), with human faces. The number of images that led to the creation of each prototype varied due to availability during photographic collection ($M = 6.67$, $SD = 2.46$). Although the number of faces per composite was lower than numbers used in recognition research (e.g., Burton et al., 2005), it was also the case that our facial images have already been selected for similar viewpoint, lighting, and neutral expression.

These 12 composites were cropped to show the head with only a small amount of neck/body and background remaining (see Figure 1). Images were approximately 350 x 400 pixels in size, or about 9 x 10cm on the screen.

Procedure

As in Study 1, participants were shown the images on the computer screen one at a time and instructed to rate them on a scale of 1 (very low) to 7 (very high). The stimuli were rated for dominance and health. The characteristics were blocked separately, and the order of block presentation was counterbalanced between participants. Trials appeared in randomized order for each participant.

Results and Discussion

For each participant, we produced a measure of accuracy by correlating their ratings for each characteristic with the chimpanzees' profiles for that characteristic. We then applied Fisher's transformation to these values. We found accuracy significantly above chance for both dominant, mean $z = .31$; $t(29) = 8.36$, $p < .0001$; and healthy, mean $z = .46$; $t(29) = 7.81$, $p < .0001$. Therefore, participants produced accurate judgments using prototype images, providing additional evidence that this ability cannot be explained by idiosyncrasies within individual photographic images.

We also compared accuracy in Study 1 with these results in order to investigate how performance may differ between individual photographs and composite images. Transformed z scores for Studies 1a and 1b were combined since the methodologies were identical for collecting dominant and healthy ratings. These were then compared with the transformed z scores discussed above for these two characteristics. We found only marginal effects of the different stimulus presentations. We found that accuracy in judging health did not differ between the two types of stimuli, $t(105) = 1.87$, $p = .064$; although there was a trend for individual images (mean $z = .58$) to produce higher accuracy than composites (mean $z = .46$). For dominant judgments, participants performed better with the composites, $t(105) = 2.00$, $p = .048$; with composite images (mean $z = .31$) producing higher accuracy than individual images (mean $z = .22$). In these experiments, identification accuracy was therefore comparable, whether we measured performance as the average rating given to multiple images of the same individual, or as the single rating given to the average image

of an individual.

General Discussion

Previous research has shown that information relating to extraversion is present in chimpanzee faces and can be accurately perceived by humans based only on static, non-expressive cues (Kramer et al., 2011). The results of the current experiments replicate and extend these findings by demonstrating that in addition to characteristics loading onto extraversion (dominant, sociable, active, solitary), information regarding an individual's emotional stability (independent, fearful), agreeableness (sympathetic), and health are present in facial cues alone. These socially-relevant traits have been previously shown to be present and identifiable in human faces (Kramer and Ward, 2010), consistent with the hypothesis that humans and chimpanzees have similar cues of personality and other traits in the face (Kramer et al., 2011). By using a new group of chimpanzees, along with two stimulus types in order to investigate the presence of information, we further support and extend previous evidence of these personality cues.

In addition to aspects of personality, we found that health information was also available from the chimpanzee face. Cues to health in human faces include averageness (Rhodes et al., 2007), symmetry (Grammar and Thornhill, 1994), sexual dimorphism (Perrett et al., 1998), skin color/texture (Stephen, Coetzee, Law Smith, and Perrett, 2009), and facial adiposity (Coetzee, Perrett, and Stephen, 2009). Evidence now suggests that health information is present in human faces (Kramer and Ward, 2010; Little, McPherson, Dennington, and Jones, 2011). It is unclear as to which, if any, of these may be potential cues in the chimpanzee face given that much information may be obscured by dark facial hair. However, research has shown that there are sexually dimorphic shape differences in bone development in the chimpanzee face (Cobb and O'Higgins, 2007) that may be sources of information. In addition, facial fluctuating asymmetry has already demonstrated links with health in chimpanzees (Sefcek and King, 2007).

We obtained health records (diaries of illnesses, injuries, etc.) from the zoo for the one and a half years prior to the collection of zoo employee ratings in order to explore the basis of the employees' health ratings. The number of events for each chimpanzee, including cuts and scrapes, colds, etc., was non-significantly correlated with mean zoo employee ratings for 'healthy', $r(10) = .39$, $p = .216$. However, we found no relationship between the total number of events and participants' ratings of health (mean $z = .06$), suggesting that unfamiliar raters used information relating to other aspects of the chimpanzees' health when forming their accurate impressions. Interestingly, the number of cuts was related to employee ratings of dominance, $r(10) = .37$, $p = .237$, and to participants' ratings of dominance, mean $z = .58$; $t(35) = 14.23$, $p < .0001$. Given the simplistic nature of the records, and the small sample size, we do not wish to place too much emphasis on the statistical significance (or lack of) in these exploratory findings, but we do suggest these relationships are promising and warrant further investigation.

The results of the second study using composite photographs showed little difference in terms of the availability of information regarding dominance and health, with cues produced by two individual photographs providing similar information to signals from

averages of multiple photographs of the same individual. This suggests that these two methods effectively produce the same outcome and further support the idea that useful information in the face was not the product of idiosyncrasies in images due to pose, lighting, etc.

In the current work, chimpanzee facial cues provided information to untrained observers about age but not gender. While perceptions of both these characteristics correlated with judgments of personality and health traits, they did not provide a complete explanation for the presence of personality information that was accurately assessed. Judgments of human faces also follow similar trends to the ones found here, with raters associating masculine faces with increased dominance (Perrett et al., 1998) and age (Keating, Mazur, and Segall, 1981).

We therefore find it an intriguing yet plausible hypothesis that chimpanzees will be able to extract and use personality and health information from the faces of their conspecifics. Currently, there is no direct evidence to support this hypothesis, but we believe this hypothesis is plausible and testable for several reasons.

First, as we have shown here, there is such information present in the chimpanzee face. That is, personality cues are available. Second, chimpanzees appear to be sophisticated face processors, attending to conspecific faces and receiving socially-relevant information from them. Chimpanzees' first fixations are on the face when shown photographs of other chimpanzees, and the face region is viewed more intensively than other parts of the body (Kano and Tomonaga, 2010). Further, chimpanzees are able to use facial information from unfamiliar conspecifics in order to discriminate individuals (Parr et al., 2000), facial expressions (Parr, 2003), and to determine relatedness (Parr et al., 2010). Although we do not yet know how personality is visually cued from the face, unless this information is cued in a way radically different from facial identity and facial expressions, then it seems chimpanzees would likely have the cognitive resources needed to extract and use personality cues. Third, being able to predict the stable behavioral biases of other group members (i.e., their personalities) seems like a useful social advantage that makes personality cues valuable. However, further research is needed before we can determine whether (and how) chimpanzees might use these potential cues to the behavior of their conspecifics.

Interestingly, our chimpanzee group may represent particular differences when compared with other captive groups. Out of 12 individuals, half are males, which may produce a specific social hierarchy and structure. While it is not clear how the balance of males and females within social environments affects both personality development and the use of cues, evidence suggests, for example, that the presence of multiple adult males may help lower the frequency of aggressive acts (Ross, Bloomsmith, Bettinger, and Wagner, 2009).

Using a different group of chimpanzees, and two methods of minimizing the effects of individual photographic images, we have shown that socially-relevant traits relating to extraversion, emotional stability, agreeableness, and health, are present in the chimpanzee face. An important aim for future research is to determine whether chimpanzees can themselves accurately interpret and use this information.

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