

Bangor University

DOCTOR OF PHILOSOPHY

Facial Signals of Personality in Humans and Chimpanzees

Kramer, Robin

Award date:
2012

Awarding institution:
Bangor University

[Link to publication](#)

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Download date: 23. Feb. 2025

Facial Signals of Personality in Humans and Chimpanzees

Robin S. S. Kramer

School of Psychology

Bangor University

Bangor, UK



PRIFYSGOL
BANGOR
UNIVERSITY

Thesis submitted for the degree of Doctor of Philosophy in Psychology

Committee Members:

Prof. Robert Ward, Supervisor

Dr. Erin Heerey, Second Supervisor

Dr. David Ingledew, Chair

DECLARATION STATEMENTS

Details of the Work

I hereby agree to deposit the following item in the digital repository maintained by Bangor University and/or in any other repository authorised for use by Bangor University.

Author Name:

Title:

Supervisor/Department:

Funding body (if any):

Qualification/Degree obtained:

This item is a product of my own research endeavours and is covered by the agreement below in which the item is referred to as “the Work”. It is identical in content to that deposited in the Library, subject to point 4 below.

Non-exclusive Rights

Rights granted to the digital repository through this agreement are entirely non-exclusive. I am free to publish the Work in its present version or future versions elsewhere.

I agree that Bangor University may electronically store, copy or translate the Work to any approved medium or format for the purpose of future preservation and accessibility. Bangor University is not under any obligation to reproduce or display the Work in the same formats or resolutions in which it was originally deposited.

Bangor University Digital Repository

I understand that work deposited in the digital repository will be accessible to a wide variety of people and institutions, including automated agents and search engines via the World Wide Web.

I understand that once the Work is deposited, the item and its metadata may be incorporated into public access catalogues or services, national databases of electronic theses and dissertations such as the British Library’s EThOS or any service provided by the National Library of Wales.

I understand that the Work may be made available via the National Library of Wales Online Electronic Theses Service under the declared terms and conditions of use (<http://www.llgc.org.uk/index.php?id=4676>). I agree that as part of this service the National Library of Wales may electronically store, copy or convert the Work to any approved medium or format for the purpose of future preservation and accessibility. The National Library of Wales is not under any obligation to reproduce or display the Work in the same formats or resolutions in which it was originally deposited.

Statement 1

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless as agreed by the University for approved dual awards.

Signed

Date

Statement 2

This thesis is the result of my own investigations, except where otherwise stated. Where correction services have been used, the extent and nature of the correction is clearly marked in a footnote(s).

All other sources are acknowledged by footnotes and/or a bibliography.

Signed

Date

Statement 3

I hereby give consent for my thesis, if accepted, to be available for photocopying, for inter-library loan and for electronic repositories, and for the title and summary to be made available to outside organisations.

Signed

Date

Statement 4

I agree to deposit an electronic copy of my thesis (the Work) in the Bangor University (BU) Institutional Digital Repository, the British Library ETHOS system, and/or in any other repository authorised for use by Bangor University and where necessary have gained the required permissions for the use of third party material.

Signed

Date

In addition to the above I also agree to the following:

1. That I am the author or have the authority of the author(s) to make this agreement and do hereby give Bangor University the right to make available the Work in the way described above.
2. That the electronic copy of the Work deposited in the digital repository and covered by this agreement, is identical in content to the paper copy of the Work deposited in the Bangor University Library, subject to point 4 below.
3. That I have exercised reasonable care to ensure that the Work is original and, to the best of my knowledge, does not breach any laws – including those relating to defamation, libel and copyright.
4. That I have, in instances where the intellectual property of other authors or copyright holders is included in the Work, and where appropriate, gained explicit permission for the inclusion of that material in the Work, and in the electronic form of the Work as accessed through the open access digital repository, or that I have identified and removed that material for which adequate and appropriate permission has not been obtained and which will be inaccessible via the digital repository.
5. That Bangor University does not hold any obligation to take legal action on behalf of the Depositor, or other rights holders, in the event of a breach of intellectual property rights, or any other right, in the material deposited.

That I will indemnify and keep indemnified Bangor University and the National Library of Wales from and against any loss, liability, claim or damage, including without limitation any related legal fees and court costs (on a full indemnity bases), related to any breach by myself of any term of this agreement.

Signed

Date

ACKNOWLEDGMENTS

I would like to thank my friends and office mates, Alex Jones and Danni Shore, for dealing with me for so long. And a huge thank you to my supervisor, Rob, who has been a great supporter of my research, even of the more bizarre ideas I've had. His studentship allowed me to pursue my ideal career, and for that, I will always be grateful.

And thank you to Flow and Jake, who provided some much needed fun and relaxation over the last few months.

In memory of Bob.

PUBLICATIONS

The three published journal articles, featured as chapters in this thesis, are:

1. **Kramer, R. S. S., & Ward, R.** (2010). Internal facial features are signals of personality and health. *The Quarterly Journal of Experimental Psychology*, *63*, 2273-2287.
2. **Kramer, R. S. S., & Ward, R.** (2011). Different signals of personality and health from the two sides of the face. *Perception*, *40*, 549-562.
3. **Kramer, R. S. S., King, J., & Ward, R.** (2011). Identifying personality from the static, nonexpressive face in humans and chimpanzees: evidence of a shared system for signaling personality. *Evolution and Human Behavior*, *32*, 179-185.

In all cases, I collected the data and contributed the majority of writing to the final publication. My supervisor advised during the analyses, and helped with the article writing. In (3), the middle author contributed the photographic stimuli and the chimpanzee personality information.

All published material is included here with the permissions of the publishers.

CONTENTS

Declaration statements	i
Acknowledgements	iv
Publications	v
Summary of PhD	vii
Chapter 1: Introduction	1
Chapter 2: Facial signals of personality and health	11
Chapter 3: Signals of personality and health in hemifaces	31
Chapter 4: Personality signals in the chimpanzee face	49
Chapter 5: General Discussion	63
References	73
Appendix	89

SUMMARY OF PHD

Recent evidence has begun to demonstrate that information regarding socially relevant traits is available from the static, neutral human face. In the current thesis, we replicated and extended previous research, showing that signals of personality and health were received by unfamiliar others. Further, these signals remained when information was limited to internal facial features, providing initial evidence of the location of these signals and the differing contributions of external and internal facial characteristics.

By investigating the signal content of hemifaces, split vertically down the midline, we found asymmetries in the information signalled by the two sides of the face. While previous research has highlighted the role of the left hemiface in transitory signals of expression, we found that the right hemiface signalled more information regarding temporally stable personality traits.

Given the similarities between humans and chimpanzees in facial morphology, face processing, and personality structure, we hypothesised an evolved system for signalling personality information that both species share. We provided the first evidence that personality information, in particular relating to dominance and extraversion, was indeed present in the chimpanzee face and could be accurately perceived by human observers. Our results support the idea that humans and chimpanzees share a system for signalling socially-relevant information from the face that dates back to our last common ancestor around six million years ago.

CHAPTER 1: INTRODUCTION

Faces represent one of the most significant types of stimuli that we encounter. Given that humans are a social species, it is no surprise that the face captures our attention in natural scenes (Fletcher-Watson, Findlay, Leekam, & Benson, 2008) and is preferred over nonface stimuli from only a few weeks of age (Mondloch et al., 1999). The importance of faces in our daily lives is undisputed.

During social interactions and in a laboratory setting, we make judgements about the personalities of strangers from their facial appearance (Zebrowitz & Montepare, 2008). We do this rapidly and with minimal information (Willis & Todorov, 2006), and we believe that the face provides a useful source of information about a person's character (Hassin & Trope, 2000). Personality attribution provides an important function, serving to guide our actions through the attempted prediction of other people's behaviours. As such, the obvious question to ask is whether these perceptions actually contain a 'kernel of truth' (Berry & Wero, 1993).

Human personality structures

By personality, I refer to stable, context-general, behavioural biases. The current thesis focuses on the five-factor model of personality (Norman, 1963; Tupes & Christal, 1961). However, there are numerous other models evidenced in the literature (e.g., a three-factor structure; Eysenck & Eysenck, 1985), all representing attempts to explain individual variations in people's personalities. While researchers fail to reach unanimity regarding the best way to describe human personality, I have chosen to use the five-factor model simply for want of a better alternative. There is a great deal of evidence supporting this model (see below), and five factors appear to provide a useful balance between traits that are too general and too specific. Further, and perhaps most importantly, the few initial studies investigating personality from static facial images also used this type of structure (Little & Perrett, 2007; Penton-Voak, Pound, Little, & Perrett, 2006). While the current thesis does not attempt to resolve the issue of correctly describing the structure of personality, if accuracy in predicting personality from the face using this model is found, such results might be considered support for the five-factor model.

Determining accurate perceptions of personality

It is important to understand exactly how we can demonstrate accuracy in perceptions of personality. In order to determine whether unfamiliar observers can produce accurate ratings or judgements, we require personality profiles of the individuals to be judged in order to make the relevant comparisons. In the current thesis, we used self-report measures of Big Five personality traits, e.g., the Mini-IPIP (IPIP: International Personality Item Pool) personality inventory (Donnellan, Oswald, Baird, & Lucas, 2006). Behavioural genetics studies estimate heritability coefficients for individual personality traits to be 0.40–0.60 (Bouchard & Loehlin, 2001), and human models show cross-cultural and even cross-species generalisation of personality factors (Gosling & John, 1999). Further, self-report measures of Big Five traits show internal consistency (Gow, Whiteman, Pattie, & Deary, 2005), agreement across measures (Paunonen, 2003), agreement with reports by others (Connolly, Kavanagh, & Viswesvaran, 2007), correlations with measures of personality disorders (Reynolds & Clark, 2001; Saulsman & Page, 2004), and validity in predicting complex real-world behaviours and outcomes (Paunonen & Ashton, 2001; Tett, Jackson, & Rothstein, 1991). As such, we consider self-report measures as representing actual personality profiles in Chapters 2 and 3, against which we are then able to compare strangers' judgements.

Perceptions from facial appearance

There are two traits that have received the most attention from previous researchers, and seem to affect our judgements of others with regard to facial appearance: attractiveness and babyfacedness (Zebrowitz, 1999). A wealth of research has demonstrated that those who we perceive to be attractive are also assumed to score highly on other positive traits like warmth, friendliness, and intelligence (Feingold, 1992). This 'halo effect' (Dion, Berscheid, & Walster, 1972) describes a clustering of positive trait judgements when forming our initial impressions of others. Although these impressions do not testify to the person's actual personality and behaviour, such assumptions still have significant outcomes in terms of hiring decisions (Marlowe, Schneider, & Nelson, 1996), job earnings (Hamermesh & Biddle, 1994), and even receiving help from strangers (Benson, Karabenick, & Lerner, 1976).

Related, our impression formation is also affected by how babyfaced someone is, i.e., how child-like their facial features are. For example, people with a relatively high forehead or large eyes (Sternglanz, Gray, & Murakami, 1977) are perceived to be more babyfaced. We know that people

with more neotenous faces are assumed to be more naive and kind (Berry & Zebrowitz McArthur, 1985) - basically, possessing qualities that are associated more with children in comparison with adults. Again, although these assumptions are unrelated to accuracy, they still produce real-world outcomes. For instance, babyfaced individuals are more likely to be exonerated when charged with intentional crimes (Montepare & Zebrowitz, 1998).

These examples of personality perceptions represent a separate, though related, area of research to the one this thesis focuses on. The current research investigates the notion of accuracy, i.e., what perceptions of people, based upon their faces, are actually correct? We know that temporary and more controllable facial expressions, such as smiles and frowns, affect subsequent judgements. For example, wearing an angry expression on your face causes others to perceive you as more dominant (Knutson, 1996). However, this research investigates static facial morphology, which is a more stable representation of our appearance in that it is far less under our control. I acknowledge that when facial photographs are obtained, the person is still able to pose to some extent, but by specifying a neutral expression, face forward, and eyes looking directly into the camera, we minimise this freedom as much as possible. As such, neutral or non-expressive photographs are used in order to explore what information is contained in the human face.

Information present in the face

Given that we judge people based on facial appearance and behave accordingly towards them, it is important to ascertain what actual information is present in the faces of strangers. With a resurgence in research into this question in recent years, we now know that neutral facial appearance provides a great deal of socially-relevant information above and beyond the most salient traits (sex, age, and race). Evidence has demonstrated that unfamiliar observers are able to accurately perceive cues to personality traits (Little & Perrett, 2007; Penton-Voak et al., 2006; Shevlin, Walker, Davies, Banyard, & Lewis, 2003), health (Coetzee, Perrett, & Stephen, 2009; Little, McPherson, Dennington, & Jones, 2011), sexual strategies (Boothroyd, Cross, Gray, Coombes, & Gregson-Curtis, 2011; Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008), sexual orientation (Rule, Ambady, Adams, & Macrae, 2008; Rule, Ambady, & Hallett, 2009), trustworthiness (Stirrat & Perrett, 2010), aggression (Carré & McCormick, 2008; Carré, McCormick, & Mondloch, 2009), and dominance (Mueller & Mazur, 1997). Indeed, the face even provides information which allows us to accurately predict such real-world category memberships as Democrat versus Republican (Rule & Ambady, 2010), and Mormon versus non-Mormon (Rule,

Garrett, & Ambady, 2010). Given the origins of personality prediction from the face as an attempt to identify criminal tendencies, it is particularly fitting that recent evidence suggest that we can accurately distinguish violent from non-violent sex offenders (Stillman, Maner, & Baumeister, 2010), and even convicted criminals from non-criminals (Valla, Ceci, & Williams, 2011). As such, we can conclude that the faces of strangers represent a rich source of socially-relevant information that viewers are able to accurately perceive.

Facial information as signals vs. cues

While there is no question that socially-relevant information is present in the face and picked up on by observers, there is some debate as to its nature and origins. In the animal communication literature, a ‘cue’ is considered to be any feature of the world (animate or inanimate) that can be used to decide what to do (Hasson, 1994). As such, the static faces of others can be considered cues. However, if a cue has evolved *because* of its affect on others then it is a special type of cue, termed a ‘signal’ (Maynard Smith & Harper, 2003). Clearly, it is difficult to state with complete certainty why a specific cue has evolved. Further, signals are often evolved from cues that have been the focus of selection (Johnson, 2010), and subsequently, may be at any point on the theoretical pathway from cue to signal (Wyatt, 2010). For example, a receiver may have successfully evolved a response to a cue, and in turn, the sender may be in the process of evolving to take advantage of this response.

While static facial information cannot be conclusively termed a signal, there is evidence in favour of this argument. Evolution seems to have produced humans who are well-adapted to their role of signal receiver, with specialised systems for processing human faces in the brain (Haxby, Hoffman, & Gobbini, 2000). With regard to an evolved sender, there have been intense selection pressures on the human face and skull (changes in diet, an increase in brain size, etc.) that do not appear to account for the continued presence of information contained in facial and structural characteristics (Lieberman, 2011). Finally, it is plausible that facial signals have evolved through sexual selection. Initial research has demonstrated that upper face height develops differently at puberty in males and females, and that these differences cannot be explained by sex differences in body size (Weston, Friday, & Liò, 2007). Male upper faces are shorter than expected for their size, with the suggestion that this results in an increased width-to-height ratio, a characteristic that affects facial attractiveness and has therefore been sexually selected. While it is not the intention of this thesis to solve such a complex issue, this brief overview will hopefully convince the reader that

information present in the static face can plausibly be considered a signal for the remainder of the current work.

Mechanisms linking personality and facial appearance

The next question to ask involves how this socially-relevant information is signalled. What is it that may link personality and physical appearance? There seem to be four potential accounts (Zebrowitz & Collins, 1997) and it is possible that all are at play in the emerging relationship that is evidenced in the literature. First, both psychological aspects and physical appearance are caused by a common biological basis. This accounts for the particular psychological profiles (although non-specific behavioural profiles) and facial combinations that are illustrative of Down's syndrome, Bloom's syndrome, cretinism, and fetal alcohol syndrome, for example. In addition, it is possible that sex hormones like testosterone may influence both behaviour and appearance (Mazur & Booth, 1998; Swaddle & Reiersen, 2002). Second, both are outcomes of a common environment. For instance, prolonged social contact may increase both personality and facial appearance similarities with the person in question (Zajonc, Adelman, Murphy, & Niedenthal, 1987). Third, personality aspects cause facial appearance. This may be due to one's personality leading to the higher frequency of specific expressions, which then affects facial appearance over many years (Malatesta, Fiore, & Messina, 1987). Alternatively, certain personalities may tend to seek out certain environments (e.g., dangerous activities), which produces particular effects on the face over time. Fourth, facial appearance causes personality. An example of this may be that someone with a particular facial appearance is treated a certain way by others, and this in turn causes the development of a personality type that matches the face. All four of these accounts could potentially explain how facial appearance signals personality information, and at present, little headway has been made in teasing these apart in order to determine which is more likely. Of course, it is also possible that different signals are the result of different mechanisms.

We know that there are signals in the face that are successfully received by observers but only recently has research begun to identify where in the face this information appears. Several studies have investigated the facial width-to-height ratio (WHR) as a signal of personality and behaviour. Already identified as a sexually dimorphic measure (Weston et al., 2007), with a greater magnitude in males, it is possible that this ratio has received sexual selection pressures causing variation within males that reflects traits important in mate selection. Researchers have identified males with a greater WHR (a proportionately wider face in reference to bizygomatic width) as more aggressive

(Carré & McCormick, 2008; Carré et al., 2009), more likely to exploit the trust of others (Stirrat & Perrett, 2010), and more likely to deceive and cheat (Haselhuhn & Wong, 2011). Current thinking regarding the link between WHR and these characteristics involves the ‘common biological basis’ account (see above). It is possible that increased testosterone concentrations at puberty in boys (Verdonck, Gaethofs, Carels, & de Zegher, 1999) causes facial development leading to an increased WHR (Penton-Voak & Chen, 2004). Testosterone is also linked with increased aggression, although the relationship is a complex one (for a review, see Archer, 2006). Interestingly, a greater WHR is also correlated with a higher body mass index in both males and females (Coetzee, Chen, Perrett, & Stephen, 2010). As yet, it is unclear as to how this piece of evidence fits into the larger picture.

Another potential source of facial signals is fluctuating asymmetry (FA). This refers to random deviations from perfect symmetry in normally bilateral traits, thought to be caused by developmental instability (Van Valen, 1962). A person who is able to develop symmetrically despite various stressors (Polak, 2003) will have lower levels of FA, and consequently, a more attractive face (Thornhill & Gangestad, 1999). With regard to personality traits, asymmetrical faces are *perceived* to be more neurotic, less agreeable, and less conscientious (Noor & Evans, 2003). In terms of how facial symmetry relates to a person’s *actual* personality, research has shown that extraverted individuals of both sexes have more symmetrical faces (Pound, Penton-Voak, & Brown, 2007). There is some evidence that greater symmetry is related to lower openness and agreeableness (Fink, Neave, Manning, & Grammer, 2005), although these findings were not replicated (Pound et al., 2007). Again, the mechanism linking facial symmetry and personality traits is unclear, although for example, people with lower facial FA may be treated in a certain way that then causes them to act more extraverted over time. Further complicating matters, evidence suggests that bodily FA has little or no relationship with personality traits (Hope et al., 2011). Certainly, further research is necessary before we can understand the link (or lack thereof) between facial symmetry and personality, and the current thesis goes some way towards tackling this issue.

Signalling personality from the chimpanzee face

Having established that humans demonstrate a system for signalling personality and other socially-relevant information from the static face, is it possible that this system was present before humans evolved? Our closest living relative, the chimpanzee, shares many similarities with our species and so might they also share this signalling system? The idea that chimpanzees might share a similar system to humans for signalling personality from the face seems plausible for at least three

reasons: homologous personality structures, facial morphologies, and cognitive processes regarding faces.

First, chimpanzees have stable personality structures. We know that nonhuman species can demonstrate stable, context-general behavioural biases (for reviews, see Gosling & John, 1999; Mehta & Gosling, 2008). Analyses of chimpanzee personality produced a structure similar to that of humans (King & Figueredo, 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, & Figueredo, 2000), along with both reliability (Freeman & Gosling, 2010) and validity in predicting individual, real-world behaviours (Pederson, King, & Landau, 2005).

Second, chimpanzees share a similar facial morphology to humans (Burrows, Waller, Parr, & Bonar, 2006), and also demonstrate homologous facial expressions (Parr, Waller, Vick, & Bard, 2007). Direct comparisons across species using standardised systems for coding muscle movement (ChimpFACS - Vick, Waller, Parr, Smith Pasqualini, & Bard, 2007; FACS - Ekman & Friesen, 1978) found substantial overlap in facial expressions (Bard, Gaspar, & Vick, 2011). Interestingly, chimpanzees and humans also both show a lateralisation of facial expressions, with greater involvement of the left side of the face (Fernández-Carriba, Loeches, Morcillo, & Hopkins, 2002; Sackeim, Gur, & Saucy, 1978). This line of research supports a common facial morphology across the two species, an important ingredient for a shared signalling system.

Third, both species show similar cognitive processing of face stimuli (Parr, Dove, & Hopkins, 1998; Parr, Heintz, & Akamagwuna, 2006), along with homologous specialised brain regions for face processing (Parr, Hecht, Barks, Preuss, & Votaw, 2009). Again, if both species have evolved similar specialisations for processing faces, the potential is there for a shared signal system.

In addition, it is clear that the face is an important social stimulus in nonhuman primates. 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 & Tomonaga, 2010). We now know that 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 (Boysen & Berntson, 1989; Dufour, Pascalis, & Petit, 2006; Parr, Winslow, Hopkins, & de Waal, 2000). Faces can also be used to discriminate males from females (Japanese macaques - Koba, Izumi, & Nakamura, 2009), and in-group from out-group members (capuchin monkeys - Pokorny & de Waal, 2009). Indeed, chimpanzees are able to use facial information from unfamiliar conspecifics to determine relatedness (Parr & de Waal, 1999; Parr,

Heintz, Lonsdorf, & Wroblewski, 2010), and rhesus macaque faces also contain kinship information (Bower, Suomi, & Paukner, 2011). Recently, research has shown that socially-relevant information relating to dominance and rank is present in the faces of nonhuman primates (mandrills - Setchell & Wickings, 2005; drills - Marty, Higham, Gadsby, & Ross, 2009), and that facial information can be used by others to discriminate individuals based on social status (rhesus macaques - Deaner, Khera, & Platt, 2005).

Finally, limited evidence has shown that there are already certain types of facial information that are perceived across species. Chimpanzees' spatial attention is affected by human gaze cuing (Barth, Reaux, & Povinelli, 2005; Tomonaga, 2007). Further, chimpanzees are able to recognise the faces of humans (Martin-Malivel & Okada, 2007) and vice versa (Vokey, Rendall, Tangen, Parr, & de Waal, 2004). Finally, humans are able to identify relatedness in other primates including chimpanzees (Alvergne et al., 2009; Vokey et al., 2004). Indeed, evidence has begun to demonstrate that humans process chimpanzee faces holistically, a strategy previously thought to be exclusive to other human faces (Taubert, 2009). Although more research is needed, these studies represent promising results when considering the potential for a shared signal system, and the current thesis will address specific aspects of this issue further.

Determining accurate perceptions of chimpanzee personality

In order to demonstrate that personality information is signalled from the chimpanzee face, we must first be able to measure each individual chimpanzee's 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, & Blackman, 1995; Riemann, Angleitner, & 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 & Figueredo, 1997). Chimpanzee trait ratings collected in this way have demonstrated strong convergent correlations with behavioural coding methods, as well as showing greater reliability than behavioural coding (Vazire, Gosling, Dickey, & Schapiro, 2007). In addition to high levels of interobserver consensus (Gosling, 2001; Gosling & Vazire, 2002), trait ratings have been validated against real-world behaviours and outcomes, with many non-human primates (e.g., rhesus monkeys - Capitanio, 1999; Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980; vervet monkeys - McGuire,

Raleigh, & Pollack, 1994), and in particular with chimpanzees (e.g., Murray, 2011; Pederson et al., 2005; Uher & Asendorpf, 2008). For example, ratings of aggressiveness and timidity showed correlations in the expected directions with dominance rank in wild chimpanzees (Buirski, Plutchik, & Kellerman, 1978). In addition, ratings of trait psychopathy correlated with specific behaviours in research centre chimpanzees, and these behaviours were similar to those seen in human psychopaths (Lilienfeld, Gershon, Duke, Marino, & de Waal, 1999). Primate personality has also shown relationships with underlying hormonal and other biological factors (Anestis, Bribiescas, & Hasselschwert, 2006; Champoux, Higley, & Suomi, 1997; Maninger, Capitanio, Mendoza, & 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, & Sisco, 2008). Personality measures as assessed by trait ratings have also demonstrated heritability of chimpanzee personality factors (dominance - Weiss et al., 2000; subjective well-being - Weiss, King, & Enns, 2002), and show links with specific genotypes (Hong et al., 2011). Therefore, a growing body of research has shown that chimpanzee trait ratings are measuring broad and stable behavioural biases (Vazire et al., 2007; also see Freeman & 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 Chapter 4 in order to produce a measure of accuracy.

The current thesis

Demonstrated above, there is growing evidence that humans signal socially-relevant information, including personality, from the static, neutral face. While some characteristics of this system have now been established, there are numerous questions that still remain unanswered. One particular issue that provides much scope for exploration, as outlined above, regards the details of where in the face this information is carried (Chapters 2 and 3). In addition, the above coverage of the literature shows there is reason to hypothesise that this signal system may be shared with our closest living relative, the chimpanzee (Chapter 4). Therefore, the current thesis incorporates three research chapters addressing these ideas.

Taken together, these chapters aim to make significant progress in the ongoing investigation into facial signals of personality. Chapters 2 and 3 tackle the subject of information present in the human face, the location of these signals, and potential mechanisms through which they are conveyed. Chapter 4 posits a cross-species signalling system and aims to provide initial evidence of the existence of this system.

CHAPTER 2: FACIAL SIGNALS OF PERSONALITY AND HEALTH ¹

Abstract

We investigated forms of socially-relevant information signalled from static images of the face. We created composite images from women scoring high and low values on personality and health dimensions, and measured the accuracy of raters in discriminating high from low trait values. We also looked specifically at the information content within the internal facial features, by presenting the composite images with an occluding mask. Four of the Big Five traits were accurately discriminated on the basis of the internal facial features alone (conscientiousness was the exception), as was physical health. The addition of external features in the full face images led to improved detection for extraversion and physical health, and poorer performance on intellect/imagination (or openness). Visual appearance based on internal facial features alone can therefore accurately predict behavioural biases in the form of personality, as well as levels of physical health.

Introduction

The face can be used to predict a person's behaviour. Some transient emotional states, such as surprise or fear, are indicated by motion within the face. And although we are frequently warned that appearances are deceiving, recent evidence also suggests that static properties of the face are similarly expressive. Some reviewers have suggested that the face is a visible indicator of sex hormone levels (e.g. Fink & Penton-Voak, 2002; Johnston, Hagel, Franklin, Fink, & Grammer, 2001). To the extent that sex hormones direct action, the face would then be a predictor of any such hormonally-driven behaviours. For example, Swaddle and Reiersen (2002) note that levels of testosterone in men are associated with both the development of the jaw-line and with levels of aggressive behaviour (Mazur & Booth, 1998). Shape of the jaw may therefore be an accurate predictor of dominance behaviours in men (Swaddle & Reiersen, 2002). In women, ovulation is associated with both visible changes in facial attractiveness (Penton-Voak et al., 1999), and a change in sexual interests and potential sexual behaviours (Gangestad, Thornhill, & Garver, 2002).

More recently, static properties of the face have been associated with enduring behavioural biases in the form of personality. Research has found that raters could identify certain personality

¹ This research appears in publication:
Kramer, R. S. S., & Ward, R. (2010). Internal facial features are signals of personality and health. *The Quarterly Journal of Experimental Psychology*, 63, 2273-2287.

traits of strangers (individually or in the form of composites) at a level significantly above chance, based only on a photograph of the face with a neutral expression (Little & Perrett, 2007; Penton-Voak, Pound, Little & Perrett, 2006; Shevlin, Walker, Davies, Banyard, & Lewis, 2003). Using composites based on the Big Five traits, extraversion, conscientiousness and agreeableness were identified accurately (Little & Perrett, 2007). Boothroyd, Jones, Burt, DeBruine, and Perrett (2008) have shown that indications of sociosexual orientation are also available from static face images. So not only do people make personality and other judgements on the basis of appearance and other “thin slices”, but these judgements can be accurate.

The face may also provide a visible signal of health, although the picture is not yet certain. A powerful theoretical standpoint is that preferences in attractiveness have evolved to guide mate choice. By this perspective, attractiveness should be a useful cue to traits of great adaptive importance, such as fertility and health (e.g. Grammer, Fink, Møller, & Thornhill, 2003). Significant effects of facial attractiveness and health have been found (e.g. Rhodes, Chan, Zebrowitz, & Simmons, 2003), but also a concealing effect has been reported, in that ratings of health are more accurate when effects of attractiveness are partialled out (Kalick, Zebrowitz, Langlois, & Johnson, 1998). Further examination of the database used by Kalick et al. (1998) suggested a small correlation between health and averageness (an r around $-.1$ between health and “distinctiveness”), but no relationship with face symmetry (Rhodes et al., 2001). There was no correlation of perceived femininity with actual health, but a small correlation between perceived masculinity and health (Rhodes et al., 2003). An ongoing debate is therefore the extent to which facial attractiveness indicates health, for example, there is disagreement about the importance of fluctuating asymmetry as an indicator of health (see Weeden & Sabini, 2005, and a response from Grammer, Fink, Møller, & Manning, 2005).

With these findings in mind, we decided to investigate whether faces accurately signal health and personality. Given the importance of their findings, our first aim was to replicate the main results of Penton-Voak et al. (2006) and Little and Perrett (2007), showing that aspects of personality were discernible from static facial images alone. Specifically, we looked to see whether composite images, formed from women with high and low personality trait values, could be accurately identified. For example, when presented with one composite made from the faces of extraverted women, and another composite made from introverted women, could observers identify which is which? Second, we wished to look again at the issue of health and appearance. Here we were specifically interested in the relationship between attractiveness and health (e.g. Grammer et al., 2003), but in some sense the more fundamental issue of whether health can be accurately

estimated from the face. We therefore looked to see whether composite face images from women of high and low self-reported health could be accurately identified. The use of composite images would effectively minimise any influence of fluctuating asymmetry, so that accurate health identification would have to rest on other factors.

Finally, we sought to develop a method for determining *where* in the face information relating to personality and/or health was carried. Specifically, we tested (1) whether the internal features corresponding to the area around the eyes, nose, and mouth were sufficient for trait recognition; and (2) for which traits did other, non-internal, features contribute to identification?

General methods

Experiments 1 and 2 each consisted of a short rating task of about 5 to 10 minutes. Participants completed both experiments, presented in counterbalanced order between participants. For exposition, it is simpler and clearer to consider the results of each task as separate experiments.

Stimuli: The composite images

For both experiments, composite face images were made from facial photos and inventories of personality and health, taken from a pool of 63 Caucasian women undergraduates (age $M = 21.03$, $SD = 1.94$, age unavailable for four participants). Course credit was given for participation. Each woman completed the Mini-IPIP personality inventory (Donnellan, Oswald, Baird, & Lucas, 2006) and the Short-Form 12-Item Health Survey (SF-12; Ware, Kosinski, & Keller, 1996). The SF-12 provides both a physical component summary (PCS) and a mental component summary (MCS). Digital photographs of each woman's face were taken by a professional photographer using professional-quality camera, lighting, and reflectors. Photos were constrained to reflect neutral expression, eyes on the camera; consistent posture, lighting, and distance to the camera; no glasses; jewellery, or make-up if possible; and hair back.

The 15 highest and lowest scorers were identified on each of seven traits: Big Five traits from the Mini-IPIP (agreeableness, extraversion, conscientiousness, neuroticism, and intellect/imagination), and physical and mental health (based upon the PCS and MCS sub-scales of the SF-12). Separate composite images were made for the high and low scorers using Abrosoft FantaFace Mixer, based on 112 key locations within the face and around the face outline. In

addition, an average composite face was made for the entire group of 63 women. (All composite images can be seen in Figure 1.)


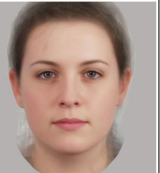
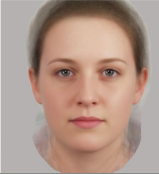


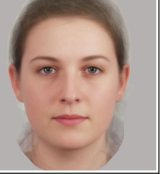

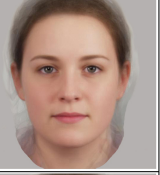
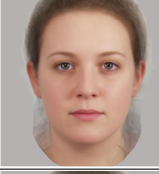
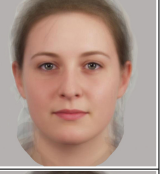





Trait	High	Low
Agreeableness		
Conscientiousness		
Extraversion		
Intellect/Imagination		
Neuroticism		
Physical Health		
Mental Health		
All females		

Figure 1. Composite faces based on self-reported personality (Mini-IPIP, International Personality Item Pool; Donnellan et al., 2006) and health (SF-12, Short-Form 12-Item Health Survey; Ware et al., 1996).

Differences between traits. Not surprisingly, the participants selected for the high and low composites differed significantly along the selected trait (all $ps < .001$), but there were also a few other differences. As might be expected, there was overlap in the measures of mental health, as assessed by the SF-12, and neuroticism. The high mental health group had significantly lower neuroticism than the low mental health group, $t(28) = 5.00, p < .001$; and likewise, the low neuroticism group had higher mental health scores than did the high neuroticism group, $t(28) = 6.77, p < .001$. The overlap of these measures simply reflects their similar domains. In addition, the high extraversion group had significantly higher mental health scores than the low extraversion group, $t(28) = 2.44, p = .021$; and the low agreeableness group had lower conscientiousness scores than high agreeableness, $t(28) = 2.17, p = .038$. The potential implications of these differences will be considered later. There were no other significant differences.

Internal face images. The composites were converted to grey-scale to minimise any skin tone differences, and cropped to produce images where only the internal features were visible (see Figure 2). By presenting only this limited region of the composites, we could explore whether the internal features of the face alone carried both health and personality information.

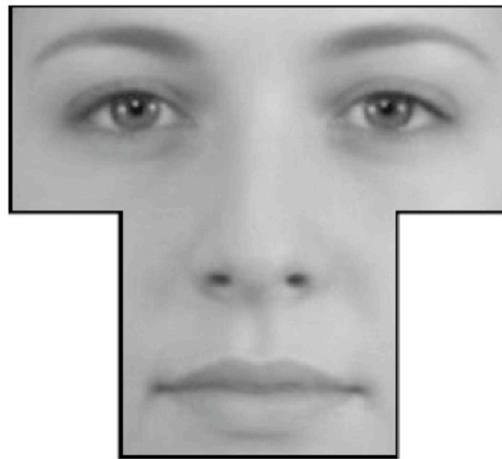


Figure 2. The “high physical health” composite, converted to black and white and cropped so that only the internal features are visible.

Experiment 1: Accuracy of trait identification from full and internal faces

Here we measured accuracy in discriminating composites made from the high and low value scorers on each trait. The high and low value composite faces were presented together, along with a

discrimination question relevant to the trait (see Figure 3). Participants judged which of the two faces better fit the question.

Method

Design

The experiment was defined by two factors describing the stimulus images: Trait (agreeableness, conscientiousness, extraversion, neuroticism, intellect/imagination, physical health, mental health) x Face Type (full face or internal features only). Face Type was varied between-participants; Trait within.

Participants

There were 131 participants (92 females; age $M = 20.99$, $SD = 2.33$), including 59 of the 63 women who contributed to the stimulus creation pool. These women plus 31 men completed the experiment using the full faces, for class credit. The remaining 41 participants (33 females) were not in the class, and completed the task using the internal face composites for printing credits. All participants were undergraduate students in the Psychology programme at Bangor University.

Procedure

On each of the 28 trials, the high and low composites for a trait were presented to the participant (image size of 489 x 489 pixels, or about 13 x 13 centimetres on a 96 dpi screen), one to the left and one to the right of centre. Viewing distance was not fixed. The task was to judge which face better suited the discrimination statement appearing beneath the composite pair. Participants indicated their answer using the mouse to click on the appropriate image, and the next trial then appeared. The experiment was self-paced, and participants were encouraged to make their best answer.

Each composite pair was presented four times, each time with a different discrimination statement. For the Big Five traits, the discrimination statements were taken directly from the four relevant questions of the Mini-IPIP inventory used for scoring the women in the stimulus pool. For physical and mental health, the discrimination statements were taken from four items of the PCS

and MCS sub-scales of the SF-12. The four items chosen were the ones producing the largest contributions to sub-scale scores for the women in our stimulus pool. For the PCS, we used discrimination statements based on items 1 (health is better), 2b (has greater difficulty climbing stairs), 3a (accomplishes less due to health problems), and 5 (pain interferes more with work). For the MCS, we used discrimination statements based on items 4a (accomplishes less due to emotional problems), 4b (works less carefully due to emotional problems), 6a (feels more calm and peaceful), and 6c (more often feels downhearted and low). The order of face pairs and questions was randomised for each participant. The presentation of high and low composites was balanced for field of presentation, both for individual participants and for the four questions used to assess each trait.

Before beginning the rating exercise, each participant also completed a computerised version of the Mini-IPIP personality inventory and the SF-12.

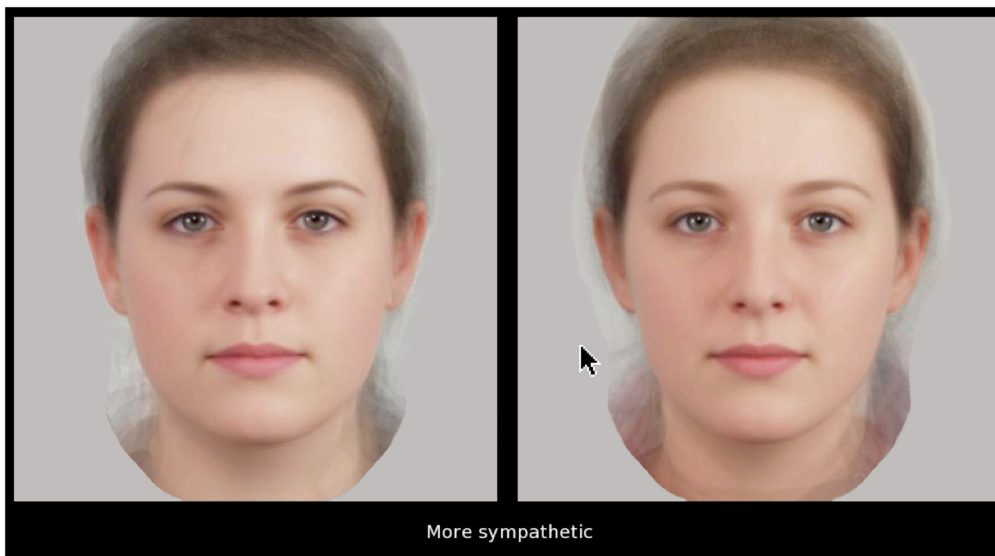


Figure 3. An example stimulus display. Participants clicked on the face that better matched the discrimination statement.

Results and discussion

There were three main findings. First, we replicated previous results showing that many personality traits can be accurately judged from static facial features (Little & Perrett, 2007; Penton-Voak et al., 2006). Second, we found that physical health is also reflected in static facial composites. Third, we found that the internal features can by themselves carry much of the

information used for personality and health judgements, although there were some elaborations and exceptions to this general rule. We now consider these points in turn.

Figure 4 shows discrimination accuracy for each trait. For the most part, traits clustered into two sets: one clearly at chance levels (conscientiousness, mental health), and the other set well above chance (agreeableness, extraversion, neuroticism, and physical health, all $ps < .001$, in these cases with both full and internal faces). Intellect/imagination was an interesting exception: identification was significantly below chance levels with full faces, $t(89) = 2.27, p = .025$, yet well above chance with internal features only, $t(40) = 4.93, p < .001$. Internal features alone therefore allowed for accurate discrimination for four of the Big Five personality traits (conscientiousness was the exception), as well as physical health.

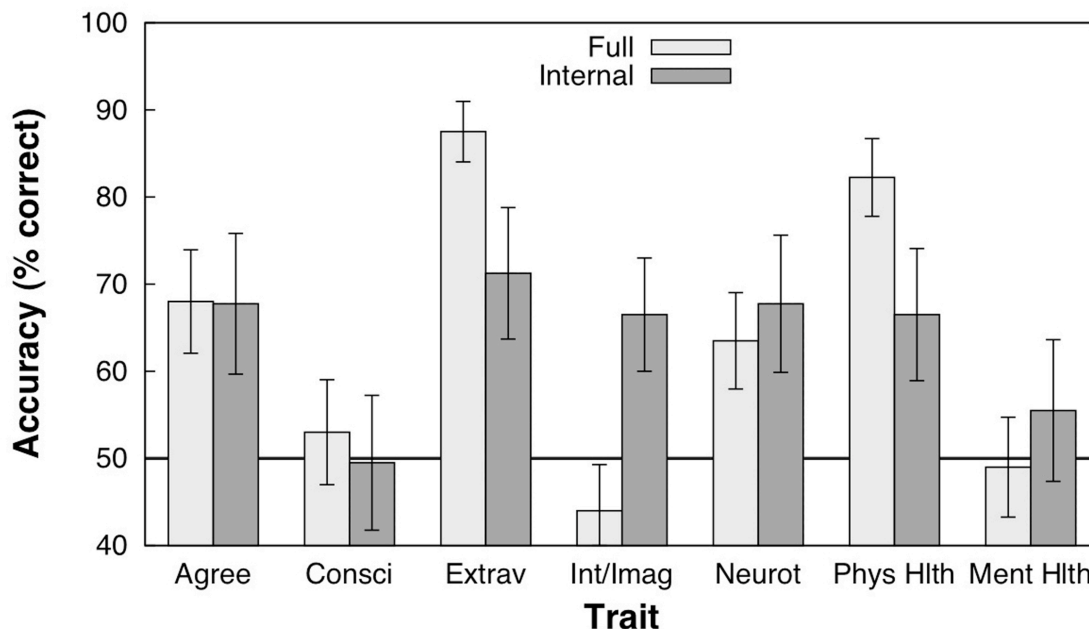


Figure 4. Accuracy on forced-choice (two-alternative) discrimination for the Big 5 personality traits and for physical and mental health, as measured by the appropriate sub-scales of the Short-Form 12-Item Health Survey (SF-12). Chance performance level indicated by line at 50%. Error bars indicate 95% confidence interval and can be used to compare conditions to baseline (i.e., error bars overlapping the 50% line are not significantly different from chance). Agree = agreeableness; Consci = conscientiousness; Extrav = extraversion; Int/Imag = intellect/imagination; Neurot = neuroticism; Phys Hlth = physical health; Ment Hlth = mental health.

Figure 5 focuses on the difference in accuracy for full and internal faces. This difference indicates the benefits or costs of external features on identification. As evident from the figure, there were three significant differences between full and internal composites. External features contributed to accurate discrimination for both physical health and extraversion, $ts(129) > 3.70, ps < .001$. For physical health, the PCS sub-scale includes questions in which excess body weight might produce lower scores (for example, “my health limits me in climbing several flights of

stairs”). Inspection of Figure 1 shows that for full faces, there is evidence of additional body weight in the outline of the low compared to high physical health faces. Cues to body weight from the face and jaw outline are not available in the internal faces, which emphasise the spatial relationships between facial parts.

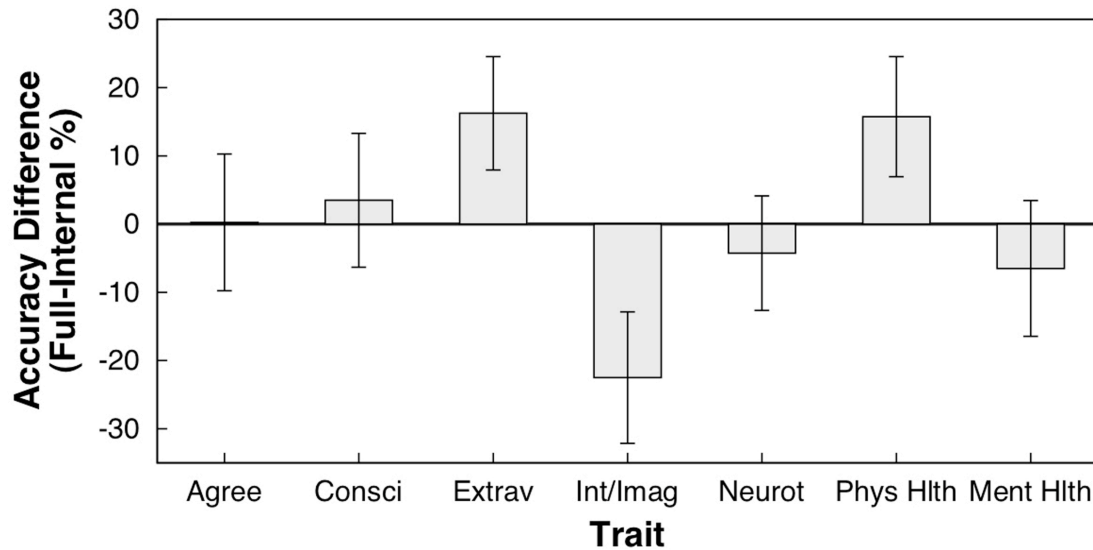


Figure 5. Difference in identification accuracy for full and internal faces. Positive bars indicate greater accuracy for full faces; negative bars indicate greater accuracy with internal features only. Error bars indicate 95% confidence intervals. Agree = agreeableness; Consci = conscientiousness; Extrav = extraversion; Int/Imag = intellect/imagination; Neurot = neuroticism; Phys Hlth = physical health; Ment Hlth = mental health.

Finally, there is the case of intellect/imagination, in which the external features actually produce systematic error in identification, compared to the internal features alone. Of the four questions on this sub-scale, two related to facility with abstract ideas, and two to imagination. We ran a two-factor ANOVA, looking at accuracy on intellect/imagination discrimination as a function of Face type (full or internal) x Question type (abstract ideas or imagination-related). External features produced interference on both estimates of imagination and abstract ideas, evidenced by the main effect of Face type, $F(1, 129) = 24.32, p < .001$. However, the two-way interaction of Face type x Question type was marginal, $F(1,129) = 3.58, p = .061$, although the form of the interaction was such that there was little effect of question type for full faces, and the benefit for internal over full faces was greater with imagination than intellect questions.

Experiment 2: Perceived attractiveness and health

Experiment 1 demonstrated accurate perception of physical health, extraversion, agreeableness, and neuroticism from the face. Internal features alone were sufficient for better than chance recognition of all these traits. However, external features, at least in combination with the internal ones, improved accuracy of physical health and extraversion judgements. In contrast, intellect/imagination, especially as tapped by imagination, was apparent from internal features, and external features were actually misleading.

Do these results reflect accurate discrimination of specific traits? Or is it possible that our results could be explained by a more general effect? The attractiveness “halo”, in which socially-desirable traits are indiscriminately applied to attractive people, is one such effect (Dion, Berscheid, & Walster, 1972). The problem with any such account is that an indiscriminate halo effect cannot by itself explain the main findings of Experiment 1, namely the cases of accurate discrimination. That is, if socially desirable traits were assigned to faces in a genuinely indiscriminate way, identification accuracy would be at chance. However, to the extent that perceived attractiveness is correlated with actual trait measures, then responses based on attractiveness could produce correct identification. Suppose, purely for illustration, that attractive people simply had the socially desirable values of the traits that were accurately identified. That is, suppose that attractive women were more extraverted, more agreeable, less neurotic, and physically healthier than less attractive women. Observers could then perform well simply by assigning the more attractive face the more desirable trait. Other kinds of global characteristics might similarly collect socially desirable trait values. For example, given the potential importance of health in problems of mate choice, it might also have been the case that socially desirable traits co-varied with healthy appearance. Given the theoretical interest in the relationship between attractiveness and health outlined earlier, and the importance of perceived health in other contexts (Kramer, Arend, & Ward, 2010), we were interested in a possible health “halo”, in which socially desirable traits might be attributed according to perceived health.

In this experiment, we looked at how discrimination performance in Experiment 1 related to the attractiveness of the different composites, and to the perceptions of their physical health. However, it may be important to re-emphasise that we are not investigating a type of halo effect in which raters are indiscriminately applying socially-desirable traits to attractive people. Instead, we are looking at the possibility that people who are rated as attractive (or healthy-looking) actually have socially-desirable traits.

Method

Design

The experiment was defined by two factors describing the stimulus images: Trait (agreeableness, conscientiousness, extraversion, neuroticism, intellect/imagination, physical health, mental health) x Face Type (full face or internal features only). Face Type was varied between-participants; Trait within.

Stimuli

The same images were used as in Experiment 1.

Participants

As described previously, all participants from Experiment 1 took part in this experiment.

Procedure

Participants rated single face images for physical health and attractiveness, in separate blocks. Images were presented one at a time in the centre of the screen, the same size as in Experiment 1. Under the image would appear a reminder phrase indicating the task for that block (e.g. “How attractive is this face?”), and under that reminder, a written 7-item scale (e.g. Very Unattractive; Unattractive; Slightly Unattractive; Average; Slightly Attractive; Attractive; Very Attractive). A similar scale was used for physical health ratings (Very Unhealthy; Unhealthy; Slightly Unhealthy; Average; Slightly Healthy; Healthy; Very Healthy). We also included a similar block in which participants rated relationship preference for the face, but technical errors in presentation of the scale invalidated subsequent analysis. Participants clicked on the appropriate rating with the mouse, and the next image then appeared.

Blocks were presented in counterbalanced order across participants. Prior to each block of trials, an instruction screen appeared showing an array of the faces about to be rated, and instructions on the rating task to be performed (e.g. “In this section you will be judging the

ATTRACTIVENESS of the faces above. Please take a moment to consider the range of attractiveness in these faces.”)

Results and discussion

We first wanted to confirm that ratings were equivalent for participants familiar and unfamiliar with the women in the stimulus pool. We did not expect any difference, as in a composite of 15 faces, the identities of the individual faces seemed impossible to discern. Other reports have suggested that individual faces are effectively disguised within composites of even six faces (Little & Hancock, 2002). When we correlated the ratings given by the two groups to each of the 15 face stimuli, we found high correlations both for attractiveness, $r(13) = .91, p < .001$, and for physical health, $r(13) = .75, p = .001$. In addition, the two groups did not differ on attractiveness ratings, $t(14) = .27, p = .793$, or health ratings, $t(14) = .60, p = .556$. The ratings of the two groups were therefore combined in further analyses.

There was general agreement in the attractiveness ratings, and to a lesser degree, the health ratings, given to the full and internal faces. For attractiveness, the correlation between the mean ratings given to each full and corresponding internal face image was $r(13) = .66, p = .008$; the agreement on health was marginal, $r(13) = .47, p = .077$.

However, our main focus is on the detailed relationship between accuracy of trait discrimination and the health and attractiveness ratings, as computed separately for full and for internal face images. Below, we present the complete results for each rating (attractiveness and health), and then selectively highlight interesting findings. To summarise, attractiveness and perceived health appear to be honest signals of extraversion and physical health, even when information is limited to internal face features. However, there are numerous cases in which discrimination performance and ratings of these signals appear to be independent.

Attractiveness

We first consider attractiveness ratings. Figure 6 shows the difference in the mean attractiveness rating given to the high and the low value composite for each trait. The difference is separately shown for full and internal face images.

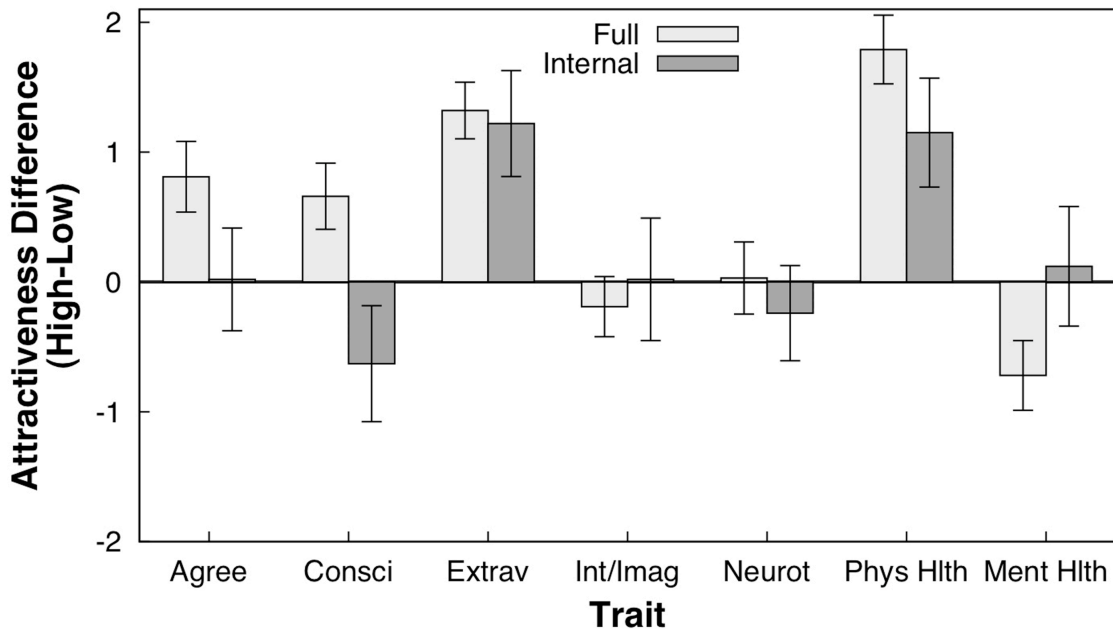


Figure 6. Difference in attractiveness for high and low trait composites. Attractiveness was rated on a 7-point scale from “very unattractive” (1) to “very attractive” (7) for all faces. Positive bars indicate greater attractiveness for high faces, negative bars indicate greater attractiveness for low faces. Error bars indicate 95% confidence intervals. Agree = agreeableness; Consci = conscientiousness; Extrav = extraversion; Int/Imag = intellect/imagination; Neurot = neuroticism; Phys Hlth = physical health; Ment Hlth = mental health.

To better understand the attractiveness differences illustrated in Figure 6, we compared differences in attractiveness with differences in discrimination accuracy in Experiment 1. These comparisons are shown in Table 1.

Table 1: Comparison of differences in attractiveness with differences in trait discrimination accuracy

Faces	Difference in attractiveness?	Discriminated trait levels?	
		Yes	No
a. Full	Yes	Agreeableness, Extraversion, Physical health	Conscientiousness, Mental Health
	No	Neuroticism	Intellect/Imagination
b. Internal	Yes	Extraversion, Physical health	Conscientiousness
	No	Agreeableness, Neuroticism, Intellect/ Imagination	Mental health

Note. Breakdown of traits according to whether high and low composites are accurately identified in Experiment 1 and whether there was a difference in attractiveness such that the more socially desirable trait pair was rated higher in attractiveness in Experiment 2.

Table 1 separately summarises the results for attractiveness and discrimination accuracy for the full and internal face stimuli. Beginning with the full faces (Table 1a), for three of the seven traits - agreeableness, extraversion, and physical health - above chance discrimination was

accompanied by significant differences in attractiveness, such that attractive composites possessed the more socially desirable trait levels. However, this relationship between attractiveness and socially desirable traits did not hold across the board. Raters in Experiment 1 were unable to accurately discriminate conscientiousness, even though the same raters in the current experiment found the high conscientiousness face significantly more attractive than the low. Similarly, raters in Experiment 1 were unable to discriminate levels of mental health, even though they found the low mental health face more attractive than the high. The reverse pattern was also found. In Experiment 1, raters were able to discriminate levels of neuroticism in the full faces, even though in the present experiment, both faces were rated equally attractive.

Attractiveness likewise does not provide a good explanation of discrimination for internal face images, summarised in Table 1b. As with the full faces, extraversion and physical health were accurately identified in Experiment 1, and also showed a significant difference in attractiveness. However, agreeableness, neuroticism, and intellect/imagination were also accurately identified from internal faces in Experiment 1, even though the high and low values of each were rated equally attractive. Finally, the low conscientiousness internal face was rated significantly more attractive than the high, but there was no accurate discrimination of these items in Experiment 1.

A consistent result therefore with both full and internal faces is that high levels of extraversion and physical health are reflected in attractive faces. In this context, it is also interesting to note that extraversion and physical health were the two traits which benefited significantly from information outside the internal faces (Figure 4). That is, there is information present in the full, and to a lesser extent, in just the internal facial features, which both is attractive to look at, and serves as an honest signal of extraversion and physical health. However, attractiveness is not associated with all discriminable personality traits, and not all discriminable personality traits are reflected in corresponding attractiveness. The pattern of accurate performance in Experiment 1 is therefore not fully explained by an association of socially desirable traits and attractiveness.

While the above analysis investigates how attractiveness judgements at the group level relate to accurate trait perception, it does not address participants' decisions at the individual level. We therefore carried out regression analyses to investigate whether differences in individual participants' ratings of attractiveness for the two composites (high minus low) predicted their accuracy i.e. did individual ratings predict subsequent discrimination? Of the seven traits for the full face judgements, only neuroticism accuracy was predicted by attractiveness ratings, $\beta = -.32, p = .014$ (Bonferroni corrected). For the internal faces, attractiveness did not predict accuracy for any of

the traits. Again, this highlights attractiveness as unable to satisfactorily explain accuracy of perception in these judgements.

Health

A similar analysis was performed for perceived physical health (see Figure 7), and differences in perceived health compared with discrimination accuracy (Table 2). For the internal faces, health and attractiveness scores were also highly correlated, $r(13) = .70, p = .004$. However, with the sole exception of mental health, $t(40) = 1.63, p = .111$, all internal face pairs were perceived to reflect significantly different levels of physical health, all $t_s(40) > 2.60$, all $p_s < .013$. In these case, accurate discrimination of many traits could therefore conceivably be explained by a “health halo”, such that healthy-looking people are not just perceived to have socially-desirable traits, but actually do possess these traits. However, again, this cannot be a complete account of our findings - the trait pairs for conscientiousness differed in perceived health but could not be accurately discriminated.

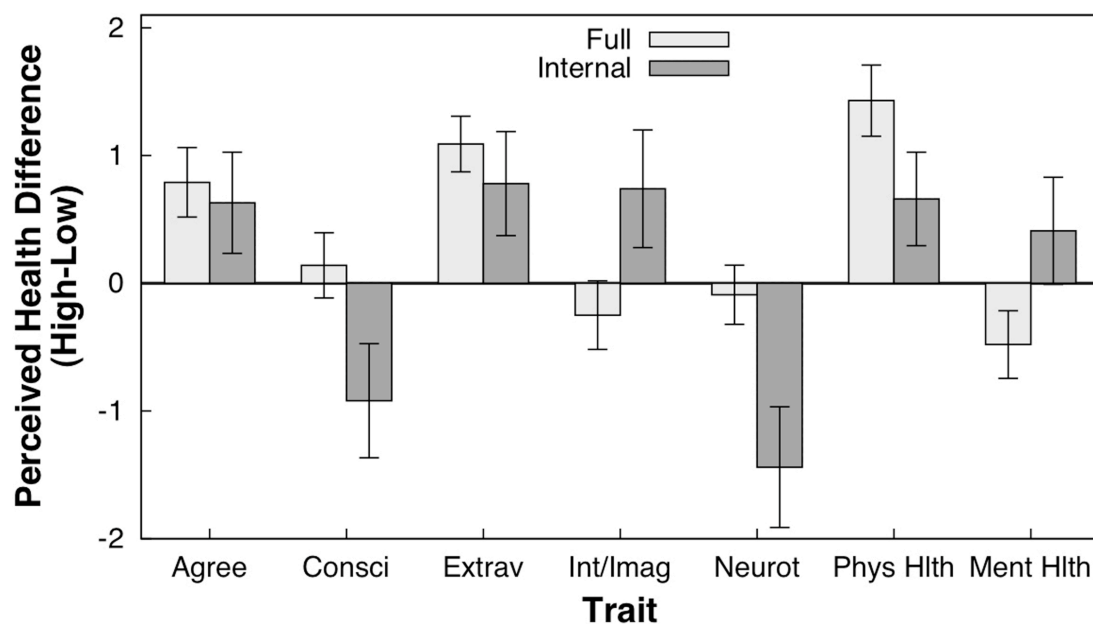


Figure 7. Difference in perceived health for high and low trait composites. Health was rated on a 7-point scale from “very unhealthy” (1) to “very healthy” (7) for all faces. Positive bars indicate greater perceived health for high faces; negative bars indicate greater perceived health for low faces. Error bars indicate 95% confidence intervals. Agree = agreeableness; Consci = conscientiousness; Extrav = extraversion; Int/Imag = intellect/imagination; Neurot = neuroticism; Phys Hlth = physical health; Ment Hlth = mental health.

Table 2: Comparison of differences in perceived health with differences in trait discrimination accuracy

Faces	Difference in perceived health?	Discriminated trait levels?	
		Yes	No
a. Full	Yes	Agreeableness, Extraversion, Physical health	Mental Health
	No	Neuroticism	Conscientiousness, Intellect/Imagination
b. Internal	Yes	Extraversion, Physical health, Agreeableness, Neuroticism, Intellect/ Imagination	Conscientiousness
	No	-	Mental health

Note. Breakdown of traits according to whether high and low composites are accurately identified in Experiment 1 and whether there was a difference in perceived health such that the more socially desirable trait pair was rated higher in perceived health in Experiment 2.

Further exceptions to a perceived-health halo are found in the data for full faces. Health and attractiveness scores for the full faces were highly correlated, $r(13) = .91, p < .001$, and the general pattern of results is similar to that for attractiveness. Table 2a shows there were three cases in the full face data in which socially desirable traits were both accurately discriminated and were also perceived as more healthy: agreeableness, extraversion, and actual physical health. But again, as with the attractiveness ratings, there were trait pairs which differ in perceived health but which were not accurately discriminated (mental health), and trait pairs which were accurately discriminated but were of equivalent apparent health (neuroticism). In summary, it seems unlikely that attractiveness or perceived health can explain all cases of accurate identification we observed in Experiment 1.

As with attractiveness, we ran regression analyses with individual ratings of perceived health as a factor predicting trait accuracy. For full faces, perceived health differences predicted accuracy for physical health only, $\beta = .38, p = .001$ (Bonferroni corrected). For internal faces, no differences in ratings predicted accuracy.

These results suggest that discriminations are not being made simply on the basis of halos relating to perceived attractiveness or apparent health. For example, neither attractiveness ratings at the group level, nor at the level of individual raters, can well explain performance across all the different traits we have measured. Our results seem to dissociate raters' perceptions of attractiveness and healthy appearance from the ability of those raters to accurately judge personality traits. A related issue is to what extent having socially desirable traits is associated with attractiveness, independent of whether the trait can be accurately discriminated. For example, our raters could not discriminate levels of conscientiousness, even though the high conscientious composite was rated as

more attractive than the low. Could it be the case that attractive, healthy-looking people will tend to have socially desirable traits, even if those traits are not accurately perceived by observers? Again, the relationship between attractiveness and socially desirable personality traits is not straightforward. For example, from our results it seems that attractive faces are more likely to reflect high than low levels of conscientiousness. However, neither attractiveness nor healthy appearance were associated with low neuroticism, or high intellect/imagination. These results suggest a more complex picture than any simple account relating a global measure such as attractiveness to social desirability for a multitude of personality traits.

General discussion

Previous work has shown that observers can accurately assess aspects of personality based on unfamiliar, static faces with neutral expressions (Little & Perrett, 2007; Penton-Voak et al, 2006). Our main results, from Experiment 1, show further that internal features of the face, specifically the areas around the eyes, nose, and mouth, carry enough information to allow accurate judgements relating to physical health, and to four of the Big Five personality factors: agreeableness, extraversion, neuroticism, intellect/imagination (cf. openness). By comparing accuracy with full faces to internal features only, our method also allowed us to identify the contribution of external features (and colour) to identification. Although external features contributed to accurate identification of health and extraversion, they actually interfered with accurate judgements of intellect/imagination.

Experiment 2 verified that accuracy did not result from attractive people simply having more socially desirable traits. That is, the traits in which the composite pair differed in attractiveness were not necessarily correctly identified, and the traits which were correctly identified did not necessarily differ in the attractiveness of the composite pair. Likewise, our results do not seem completely consistent with the possibility that healthier looking people also have simply more socially desirable personality traits than less healthy looking people. Analyses of individual predictors further demonstrated that perceived health and attractiveness, while influencing judgements, did not account for accurate perceptions of personality.

As noted earlier, there were a few cases in which our composites overlapped in traits other than those they were created for. There was no surprise that MCS and neuroticism dimensions coincided for those individuals making up the composite pairs as these scales clearly reflect similar domains. That neuroticism but not MCS was discriminated from the images is more surprising,

though this may simply reflect that the latter taps a more general domain that also includes depression, anxiety, etc. Alternatively, MCS may just be a less well validated measure of mental health. In addition, the low agreeableness group had significantly lower conscientiousness than the high agreeableness group. This may mean that agreeableness composites were more easily discriminated because they differed on two trait dimensions. However, conscientiousness was not accurately discriminated, and so it seems unlikely that this extra information would have contributed significantly to participant accuracy.

Our results provide a useful replication of the Penton-Voak et al. (2006) and Little and Perrett (2007) findings. These studies used correlations of rated and actual traits, rather than the forced-choice identification we used. Little and Perrett used composite images, as we did, while Penton-Voak et al. also used individual images. These two studies asked observers to rate the degree of a trait (e.g. agreeableness present in the image), whereas we asked observers the same questions that were used to create the personality ratings. Despite these differences in images and observer tasks, all three studies found accurate identification of agreeableness and extraversion. Like Little and Perrett, we also find accurate identification of neuroticism, although in our internal as well as full face images. Little and Perrett noted several potential advantages and disadvantages in the use of composites. One advantage is that traits consistently associated with specific visual features will have increased signal to noise ratio. The fact that neuroticism is, to date, found more easily with composite than single images suggests that the distinguishing visual characteristics for this trait are only weakly present in single images.

We have no compelling account as to why conscientiousness was accurately identified in the Little and Perrett (2007) images but not in ours. Similarly, there are differences in their study and ours in the attractiveness differences of composites. Little and Perrett only found differences between the high and low agreeableness female composites, whereas we found observed significant differences in extraversion and conscientiousness as well. This may simply reflect the reliability of trait differences across different samples but at present it is difficult to tell.

Although both Penton-Voak et al. (2006) and Little and Perrett (2007) investigated personality displays in male and female faces, our current research only explored female composites. This limitation was due to our sampling a population with a low number of males, and therefore making it impossible to produce sufficiently separate composites, and it is likely that the current results may differ to those expected from male composites. Little and Perrett found that male composites only differed significantly for extraversion, and suggest that males may contain fewer cues in the face to their actual personality than females. This idea finds limited support in the literature, which has

shown that women are believed to use more expressive and nonverbal behaviours than men (Briton & Hall, 1995), and are better nonverbal encoders of facial expressions than men (Rosenthal, Hall, DiMatteo, Rogers, & Archer, 1979). However, these relate to dynamic signals and so further research is required to demonstrate their applicability to static features.

As noted above, the use of composites could potentially lose as well as gain signals. Some previous evidence suggests that fluctuating asymmetry, in the face as well as the body, is a cue to developmental integrity and physical health (Thornhill & Møller, 1997). FA within a composite image will of course tend to be less than in any of the components. However, although FA is an unlikely cue for physical health in the composites, physical health was still accurately identified in both full and internal face images. We also noted earlier that evidence of excess body weight is much reduced in the internal images. Skin blood colouration is also associated with perceived health (Stephen, Coetzee, Law Smith, & Perrett, 2009), with increased redness linked with higher levels of blood oxygenation, although this cue was also not available in the internal face images. While we accept that skin surface properties and FA likely play a role in assessing health, our results show that other features also signal health when these cues are minimal. At present, we suggest that health is signalled through a variety of cues, including FA and colour, but also the spatial arrangement of internal face features.

We close with some admittedly speculative, but perhaps intriguing links between our results and theories of biological signal systems. In this context, we have seen that a signal, in this case, levels of socially desirable traits (such as high or low levels of agreeableness), are expressed on the face of the “sender”, and are accurately detected by the “receiver” viewing the face. Theories of biological signal systems emphasise the perspectives of both the sender and receiver: a signal must be sufficiently informative, sufficiently often, that receivers benefit from attending to it. That is, if a signal is uninformative or easily faked, there is no advantage or reason for the receiver to attend to it. Conversely, in a stable-state system, attention to a signal suggests that there is some net benefit to the receiver in attending. But this very validity opens the possibility of another selective pressure, for the sender to insert occasional deceptive messages, which benefit the sender, possibly at the expense of the receiver. That is, the receiver may be manipulated into acting against their own best interests (e.g. Dawkins & Krebs, 1978). What then keeps the system “honest”? For example, in the context of mate choice, an individual who could display false signals of exaggerated fitness might acquire a higher quality mate. In this context, the interests of the sender and receiver are not entirely opposing, but they are divergent, producing a pressure to exaggerate fitness. Why is it then that all faces do not express a socially desirable personality? A general conclusion from signal theory is

that in such cases of divergent self-interests, a signal will generally not remain informative unless it entails costs which impact more heavily on less fit individuals (“costly signals”; Grafen, 1990; Zahavi, 1975). An interesting issue may therefore be identifying costs for expressing socially desirable traits on the face.

The next step

Given this initial evidence of information in the full face, but also in the internal features alone, I decided to further investigate signal location. In the next chapter, I explored personality and health information in hemifaces. As well as considering whether hemifaces alone carried such signals, I compared accuracy from the left and right hemifaces in order to determine whether the two sides of the face signalled differently.

CHAPTER 3: SIGNALS OF PERSONALITY AND HEALTH IN HEMIFACES ²

Abstract

Previous studies demonstrate that people with different personality traits have different looking faces. We investigated whether personality and health information are differently signalled by the two hemifaces. Using composite images created from women with high and low scores on health and personality dimensions, we investigated discrimination accuracy with original and mirrored hemifaces. By comparing discrimination accuracy for particular types of hemiface, we address issues regarding both the location of information signals and how these signals are conveyed. From the hemiface stimuli, participants could accurately identify three of the Big Five traits, along with health. We found differences in which hemiface could be more accurately identified, depending on the expressed trait. Emotional stability and health were more accurately discriminated from the right hemiface, while extraversion showed higher accuracy from the left hemiface. We found evidence for differences between hemifaces related to both directional asymmetries and to other information content. Finally, our results also address ongoing debate about which side of the face is more attractive, as we found attractiveness differences between hemifaces depended upon the personality trait most clearly expressed.

Introduction

We sometimes make judgements about people based purely on their facial appearance. While society warns us against such practices, claiming that these perceptions are often unfounded, there is a growing body of evidence suggesting a level of accuracy that may explain why we do so. It is commonly accepted that expressions of emotion can be read from both static (Ekman et al., 1987) and dynamic (Bassili, 1979) properties of the face, although these are transient states that are easily faked (many studies in this area utilise posed expressions, e.g., Izard, 1971). More stable properties of the face are often linked with hormone levels, which have an effect on both morphology and behaviour. For instance, sex hormones like testosterone influence both the shape of the jaw and levels of aggression (Swaddle & Reiersen, 2002), as well as relative face width and dominance behaviours (Stirrat & Perrett, 2010). For women, ovulation affects both facial attractiveness

² This research appears in publication:
Kramer, R. S. S., & Ward, R. (2011). Different signals of personality and health from the two sides of the face. *Perception*, 40, 549-562.

(Penton-Voak et al., 1999) and sexual interests and behaviours (Gangestad et al., 2002). These effects may be apparent in a study by Boothroyd et al., (2008), who showed that indications of sociosexual orientation are accurately perceived from static face images.

There is now growing evidence that shows personality can also be accurately perceived from the static properties of the faces of strangers. Raters are able to identify personality traits from both individual (Kramer et al., 2011; Penton-Voak et al., 2006; Shevlin et al., 2003) and composite (Kramer & Ward, 2010; Little & Perrett, 2007; Penton-Voak et al., 2006) faces with neutral expressions. Composite images are produced by averaging together a group of individual photographs, therefore maintaining the defining characteristics of that group while minimising those characteristics that make each face look individual (Rowland & Perrett, 1995). By creating composites based on the 'Big Five' facets of personality, research demonstrates accurate identification of Extraversion, Agreeableness, Conscientiousness, and Neuroticism (Kramer & Ward, 2010; Little & Perrett, 2007; Penton-Voak et al., 2006) for female faces. For male faces, the story is a little less clear, with accurate perception of Extraversion (Little & Perrett, 2007; Penton-Voak et al., 2006), as well as Agreeableness and Neuroticism (Penton-Voak et al., 2006). While people tend to associate attractiveness with possession of more socially desirable traits (Dion et al., 1972), and hence facial attractiveness may play some role in accurate perception of these traits, Kramer and Ward (2010) showed that this alone did not provide a sufficient explanatory mechanism for accurate personality identification.

There is also some evidence to suggest that the face may signal health, and that this is related to attractiveness (e.g., Zebrowitz & Rhodes, 2004). However, the evidence thus far has remained inconclusive. Identified cues to health include averageness (Rhodes et al., 2007), symmetry (Grammar & Thornhill, 1994), sexual dimorphism (Perrett et al., 1998), skin colour/texture (Stephen et al., 2009), and facial adiposity (Coetzee et al., 2009). By using composites and controlling for expression, Kramer and Ward (2010) demonstrated that health could be accurately read from the face, even when some of these cues were minimal due to the removal of colour and external facial features. While the use of composites minimises fluctuating asymmetries, a potential cue to health (Weeden & Sabini, 2005), it makes any directional asymmetries even more apparent.

Although it appears that certain socially relevant traits are indeed visible in the face, it is still unclear as to what it is about the morphology that makes this possible. While accurate perception has been established with full faces, little has been done to investigate where in the face this information is carried. Kramer and Ward (2010) began to address this issue with the use of 'internal' faces, where the area containing only the eyes, nose, and mouth was visible. By

presenting these stimuli in grey-scale, they were able to demonstrate that accurate perception of Agreeableness, Extraversion, Intellect/Imagination, Neuroticism, and physical health was possible without the information provided by skin colouration and external features such as jaw shape. Indeed, in the case of Intellect/Imagination, removal of this information actually improved performance, suggesting that external features may on occasion signal deceptively.

Another way of exploring the location of information in the face involves its laterality. There is no research as yet investigating whether the right and left sides carry identical or differing information with regard to personality and health, and how this may relate to accuracy in signalling. However, there is much evidence demonstrating the existence of differences in perceptions. Note that here and throughout, we will use “left” and “right” to refer to the perspective of the stimulus faces, ie the left and right of the actor, not the viewer. It is generally accepted that the left side of the face is more emotionally expressive, even when controlling for side of presentation by utilising mirror-reversed faces (Nicholls et al., 2002). In turn, this can lead to perceptions of a more scientific and less emotional person when more of the right side of the face is visible (Lindell & Savill, 2010; ten Cate, 2002). This effect on observers’ perceptions is known by actors, who choose to show more of their left sides when asked to look emotional and more of their right when asked to look scientific (Nicholls et al., 1999). Interestingly, the left side of the body during walking is also judged to be more emotionally expressive (Roether et al., 2008). There is even evidence that the left side of the face is more emotionally expressive in other species (Fernández-Carriba et al., 2002).

Many studies explore these face-side differences by creating chimeras composed of the left side of the face combined with its mirror to produce a symmetrical and realistic face. This method accentuates lateral differences when compared with its right-side counterpart. However, inherent disadvantages of this technique include the duplication of blemishes and the appearance of unnatural lighting/shadows (Kowner, 1995). This literature has confirmed that the left side of the face expresses posed emotions more intensely (Sackeim et al., 1978) and appears more expressive, even in neutral faces (Zaidel et al., 1995). However, there is much disagreement as to whether one side or the other is perceived as healthier (left – Sitton et al., 2006; right – Reis & Zaidel., 2001) or more attractive (left – Sitton et al., 2006; right – Zaidel et al., 1995).

We decided to investigate whether the two halves of the face differently signal health and personality, and how these differences might be explained. We measured the accuracy of observers in identifying personality traits from hemiface and mirrored hemiface stimuli. Our design allowed us to make multiple comparisons in order to identify potential differences in the laterality of personality expression in the face. We considered three potential accounts: perceptual bias,

information differences between sides, and directional asymmetries. Figure 1 summarises how specific hemiface comparisons allow us to differentiate between accounts.

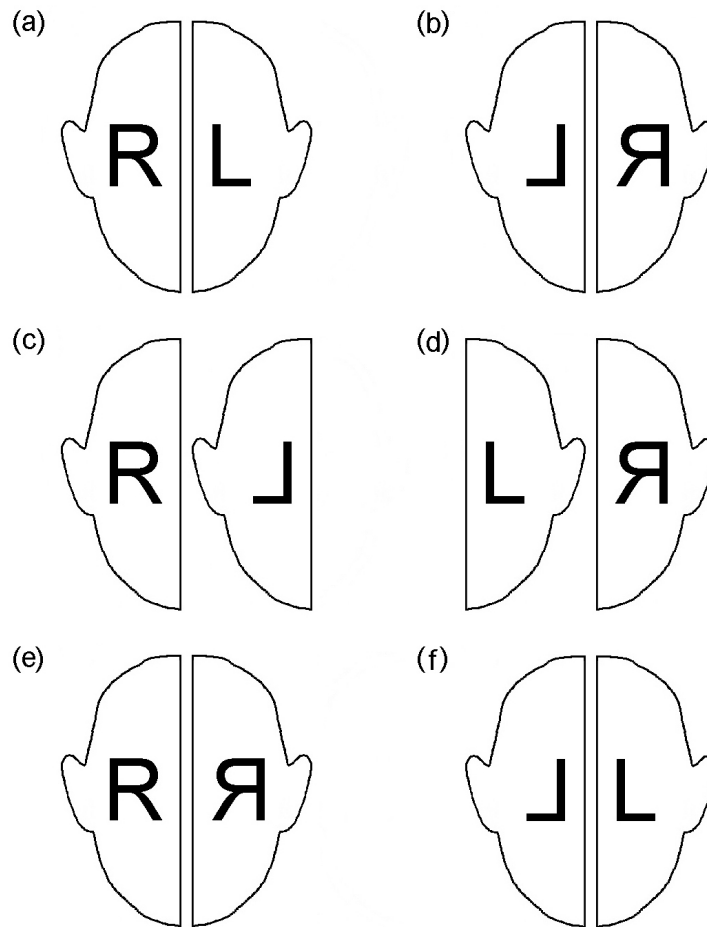


Figure 1. Different hemiface comparisons provide evidence for various accounts of performance difference. (a) Information content and perceptual bias vary; any available directional asymmetry information can be used correctly. (b) Information content and perceptual bias vary, but any directional asymmetries will be misleading. (c,d) Information content varies; some directional asymmetry information can be used correctly. (e,f) Perceptual bias varies but the information content of each hemiface is the same; some directional asymmetry information can be used correctly.

By perceptual bias, we refer to accounts in which more accurate trait judgements from one hemiface over the other reflect biases in the observer’s visual processing rather than information in the hemifaces themselves. Although “perceptual bias” in face processing is often used to describe a bias to attend to one side of full faces, a bias could also emerge for hemifaces. For example, it is frequently found that the right hemisphere shows some specialisation for face processing compared to the left hemisphere (Burt & Perrett, 1997; Le Grand et al., 2003). Specialised face processors might then be biased for face stimuli that would be typically presented in the left hemifield, that is, the actor’s right hemiface. In principle, such a bias could be found even when hemifaces are centrally presented, if the face invokes an object-based frame of reference for subsequent

processing (e.g., Hommel & Lippa, 1995).

A perceptual bias, for the viewer to more readily engage with either a left or a right hemiface, can be easily distinguished from an account in which the two hemifaces actually contain different information. For example, just as the left hemiface may contain more information about emotional state than the right hemiface (Sackeim et al., 1978), one hemiface may more accurately signal information about a personality trait.

By directional asymmetries, we refer to one, very specific sort of information difference that produces observer expectations about the information gained from each hemiface. While fluctuating asymmetries randomly deviate from perfect symmetry (e.g., right hemiface equally likely to be larger or smaller than left hemiface), directional asymmetries show a consistent bias across a population which our perceptual mechanisms have adapted to over time (Rhodes et al., 2009). For example, the right hemiface is generally larger than the left hemiface (Farkas & Cheung, 1981). Unlike other information differences, the interpretation of directional asymmetries would be disrupted under conditions of mirror reversal.

In the present study, we presented composite hemifaces that reflected real differences between people with different levels of traits. As such, we investigated whether one side of the face produced different accuracy in perceiving these traits in comparison with the other. Composite faces were used in order to more easily investigate population-wide laterality differences. Discrimination accuracy was measured using a two-alternative forced choice methodology.

Method

Participants

Thirty-two participants (25 females; mean age = 20.00 years, SD = 3.15 years) took part for course credit. All participants were students in the Psychology programme at Bangor University.

Design

The experiment was defined by three factors describing the stimulus images and presentation: Trait (Agreeableness, Conscientiousness, Extraversion, Emotional Stability, Intellect/Imagination, Health) x Face Type (original or mirrored) x Face Side (left or right of actor). All factors were varied within participants.

Stimuli: The composite images

The face images were adapted from the full-face composite images created by Kramer and Ward (2010). Here we briefly describe how those composites were made, for full details refer to Kramer and Ward (2010). A pool of 63 white European women completed a Big Five personality assessment (Mini-IPIP; Donnellan et al., 2006) and health survey (SF-12; Ware et al., 1996). Digital photographs of each woman's face were taken, constrained to reflect neutral expression, eyes on the camera; consistent posture, lighting, and distance to the camera; no glasses, jewellery, or make-up; and hair back.

The 15 highest and 15 lowest scorers were identified on each of the Big Five traits (Agreeableness, Extraversion, Conscientiousness, Emotional Stability, and Intellect/Imagination), and Health (based upon the PCS sub-scale of the SF-12). Although the Mini-IPIP specifies Neuroticism, we refer to its reverse, Emotional Stability, so that the high and low scores reflect high and low social desirability for all traits. Separate composite images were made for the high and low scorers using Abrosoft FantaFace Mixer, based on 112 key locations within the face and around the face outline. (All composite images can be seen in Kramer & Ward, 2010.) This procedure created composite face pairs reflecting low and high values on each of the six traits. Kramer and Ward (2010) found that the pairs for Extraversion, Agreeableness, Emotional Stability, and Health could be accurately identified (all $ps < .001$).

Hemiface images. Each of the 12 composites taken from Kramer and Ward (2010) was divided in half down the midline, in the midsagittal axes. For each half, a mirror image was also produced (see figure 2), to create 48 hemiface stimuli. By presenting only composite hemifaces, we could explore whether the two sides of the face carried similar or different health and personality information.



Figure 2. Example stimuli. The full face composite for high extraversion (centre) is cropped to produce (b) the right hemiface and (a) the right hemiface mirrored, along with (c) the left hemiface and (d) the left hemiface mirrored.

Procedure

On each trial, the high and low composite hemifaces were presented to the participant (image size of 175 x 445 pixels, or about 5 x 12 centimetres on screen), one above and one below the centre of the screen. Viewing distance was not fixed. The task was to judge which hemiface better suited the discrimination statement appearing to the left of the composite pair (see figure 3). Participants indicated their answer by using the mouse to click on the appropriate image, and the next trial then appeared. The experiment was self-paced, and participants were encouraged to make their best answer.

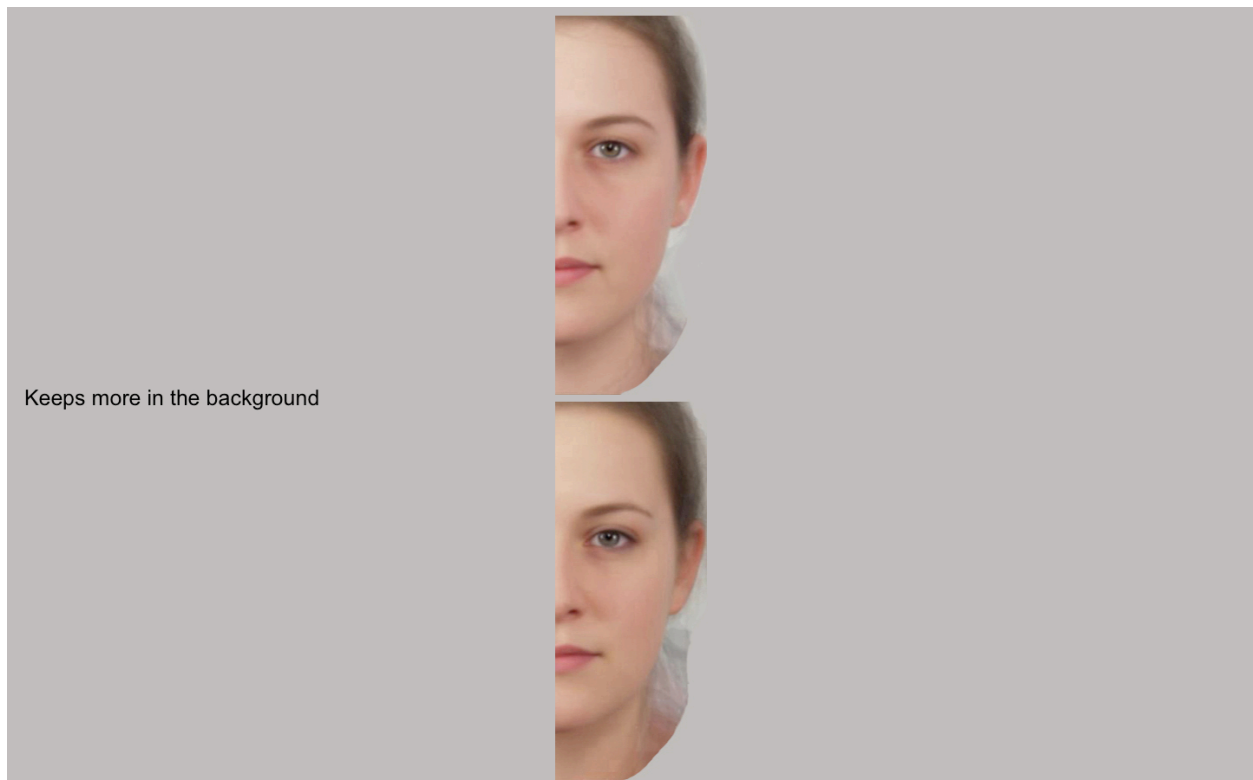


Figure 3. An example stimulus display. Participants clicked on the hemiface that better matched the discrimination statement.

Each of the 24 stimulus pairs was presented four times, each time with a different discrimination statement. For two of the discrimination statements, the correct answer was the low-value face, and for two the high-value face. We showed each of these 96 trials twice, counterbalancing the position of the stimuli so that each of the hemifaces would be correctly selected once in the upper and once in the lower screen position. For the Big Five traits, the discrimination statements were taken directly from the four relevant questions of the Mini-IPIP inventory used for scoring the women in the original stimulus creation. For Health, the discrimination statements were taken from four items of the PCS sub-scale of the SF-12. The four items chosen were the ones producing the largest contributions to sub-scale scores for the women in our stimulus pool. We used discrimination statements based on items 1 (health is better), 2b (has greater difficulty climbing stairs), 3a (accomplishes less due to health problems), and 5 (pain interferes more with work). All factors were counterbalanced. In addition, the order of trials was randomised for each participant.

After completing the discrimination task, participants rated each of the 48 hemifaces for attractiveness. Images were presented one at a time in the centre of the screen, the same size as before, and in random order. Above the image would appear the phrase “How attractive is this face?”, and under the image, a written 7-item scale (e.g., Very Unattractive; Unattractive; Slightly

Unattractive; Average; Slightly Attractive; Attractive; Very Attractive). Participants clicked on the appropriate rating with the mouse, and the next image then appeared.

Results

Overall Trait Accuracy

A 2 (Face Side: left or right) x 6 (Trait: Agreeableness, Conscientiousness, Extraversion, Emotional Stability, Intellect/Imagination, Health) x 2 (Face Type: original or mirrored) ANOVA found a main effect of Trait ($F_{5, 155} = 13.47, p < .001$), demonstrating that accuracy varied for the different traits that were included. We consider these effects in more detail below.

One main interest was in the effects of laterality. Here we found a main effect of Face Side ($F_{1, 31} = 7.22, p = .011$), with accuracy higher for the right side ($M = 58.4%$) of the face compared with the left ($M = 55.1%$). This was qualified by a Trait x Face Side interaction ($F_{5, 155} = 6.30, p < .001$). Figure 4 illustrates how accuracy was significantly higher for the right side of the face compared with the left for Emotional Stability, Intellect/Imagination, and Health (all $ps < .04$), but lower for Extraversion ($p = .005$).

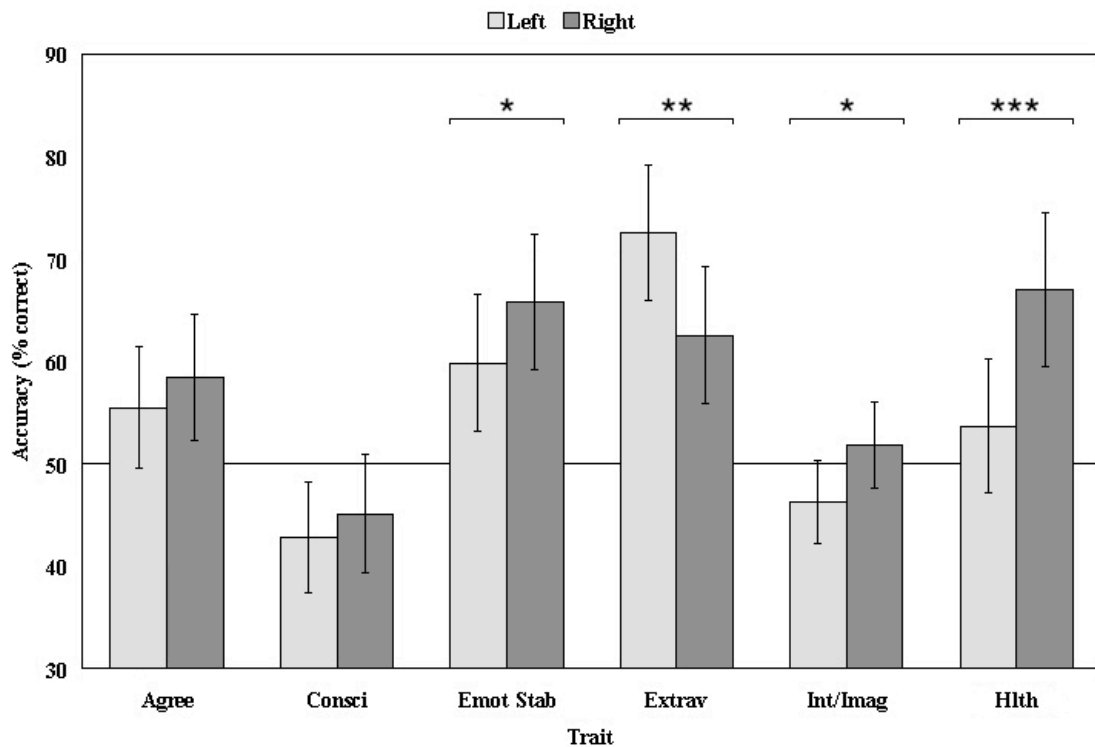


Figure 4. Accuracy on two-alternative forced-choice discrimination for the Big Five personality traits, and for Health, as measured by the PCS sub-scale of the SF-12. Chance performance level indicated by line at 50%. Error bars indicate 95% confidence interval and can be used to compare conditions to baseline (i.e., error bars overlapping the 50% line are not significantly different from chance). Agree = agreeableness; Consci = conscientiousness; Emot Stab = emotional stability; Extrav = extraversion; Int/Imag = intellect/imagination; Hlth = health. * were significantly different at an uncorrected alpha level of .05; ** at .01; *** at .001.

As figure 4 shows, Extraversion was accurately perceived on both the left ($t_{31} = 7.03, p < .001$) and right ($t_{31} = 3.79, p < .001$) sides of the face. Emotional Stability was also accurate in the left ($t_{31} = 2.97, p = .006$) and right ($t_{31} = 4.79, p < .001$) sides. Agreeableness performance was above chance for the right side of the face ($t_{31} = 2.80, p = .009$) and close to significant for the left ($t_{31} = 1.90, p = .067$). Health was above chance for the right side ($t_{31} = 4.59, p < .001$). Conscientiousness was below chance for the left side of the face ($t_{31} = 2.77, p = .009$). (All p values are uncorrected.)

The results with hemifaces are largely similar to Kramer and Ward's (2010) findings. Using full face versions of the stimuli used here, Kramer and Ward found that Extraversion, Agreeableness, Neuroticism (aka Emotional Stability), and Health were identified well above chance levels. In comparison, Conscientiousness was at chance, and Intellect/Imagination was actually identified at slightly below-chance levels.

There was also a main effect of Face Type ($F_{1,31} = 5.28, p = .029$), with original faces ($M =$

57.9%) perceived more accurately than mirrored faces ($M = 55.6\%$). This was qualified by a Face Side x Face Type interaction ($F_{1, 31} = 7.54, p = .010$), where the right side was more accurate than the left for original faces but not mirrored.

No other effects or interactions were significant (all $ps > .269$). See Table 1 in the Appendix for all mean accuracy scores separated by Trait, Face Side, and Face Type.

The focus of this experiment is to determine whether accuracy in personality identification is related to differences in the two hemifaces. Given that accuracy scores on both Conscientiousness and Intellect/Imagination were around or below chance levels for both hemifaces, we excluded these traits from the exploration that follows. We would be reluctant to draw any conclusions about mechanisms when hemifaces carried little information that could be accurately perceived anyway.

In the next sections, we look in detail at the predictions from each of three accounts outlined earlier. For the analyses that follow, we did not correct for multiple statistical tests. The comparisons we made were planned in accordance with hypotheses generated from the various accounts that we highlight. It is important to note that the different analyses complemented and supported each other, and as such, made it unlikely that our results were spurious and could have been due to the number of comparisons that were made.

Perceptual Bias

As discussed earlier, a perceptual bias account refers to biases in the observer's visual processing. Although there was an advantage for what appeared to be the right side of the face, as evidenced by the interaction of Face Side x Face Type, the perceptual bias account cannot fully explain our results. As described above, we also found a Trait x Face Side interaction, demonstrating that accuracy was not higher with one hemiface for every trait (as a perceptual bias account predicts), and instead differed between traits. Specifically, using original hemifaces (see figure 1a), we found that the original version of the right side of the face was more accurately perceived than the original left side in Health ($t_{31} = 3.70, p = .001$), and was close to significant in Agreeableness ($t_{31} = 1.99, p = .056$) and Emotional Stability ($t_{31} = 1.85, p = .074$). In contrast, the original left version was more accurate than the original right for Extraversion ($t_{31} = 2.68, p = .012$). Therefore, the original right hemiface was more accurately perceived for some traits while the original left produced greater accuracy for others.

Similarly, a perceptual bias account failed to explain our results comparing the mirrored hemifaces (see figure 1b). For Health, original right hemifaces produced greater accuracy than

original left hemifaces. A perceptual bias account would suggest a bias towards the viewer's left, therefore predicting greater accuracy for the mirrored left hemiface when compared with the mirrored right. However, this was the opposite of what we found, with the mirrored right hemiface producing greater accuracy than the mirrored left for Health ($t_{31} = 2.94, p = .006$). Likewise for Extraversion, the above results showed that the original left hemiface was more accurate than the original right, suggesting a bias towards the viewer's right side, which in turn predicts greater accuracy for the mirrored right hemiface over the mirrored left. Again our results showed the opposite pattern, with the mirrored left being more accurate than the mirrored right for Extraversion ($t_{31} = 2.10, p = .044$). Finally, given that original right hemifaces produced close to significant improvements in accuracy over original left hemifaces for Agreeableness and Emotional Stability, we would predict greater accuracy for mirrored right hemifaces over mirrored left hemifaces for these traits if a perceptual bias was apparent. However, we found no differences for these comparisons (all $ps > .29$).

In conclusion, no simple explanation of a general perceptual bias can account for this set of results, as observers did not show a consistent bias towards hemifaces that would typically appear in one visual hemifield over the other. Further, using a perceptual bias account to explain specific hemiface advantages led to incorrect predictions with mirrored hemifaces.

Information Content

By comparing an original hemiface to the mirrored version of the other hemiface (see figures 1c and 1d), we can keep any perceptual bias constant, while allowing information content to vary. In addition, directional asymmetry information can be correctly used for the hemiface that is not mirrored. The original right hemiface was more accurate than the mirrored left hemiface in Health ($t_{31} = 3.22, p = .003$) and Emotional Stability ($t_{31} = 3.88, p = .001$). In these cases, better performance can be explained by either information content present in the right but not the left hemiface, or by the use of directional asymmetries available in the right hemiface, but unavailable or even misleading in the mirrored left hemiface. However, the mirrored right hemiface led to greater accuracy than the original left hemiface for Health ($t_{31} = 2.61, p = .014$), and this can only be explained by information content unrelated to directional asymmetries since the mirrored hemiface provided no useful directional asymmetry information.

Similarly, the original left hemiface was more accurate than the mirrored right hemiface in Extraversion ($t_{31} = 2.40, p = .023$). In this case, better performance can be explained by either

information content or the use of directional asymmetries in the left hemiface. However, the mirrored left hemiface led to greater accuracy than the original right hemiface for Extraversion ($t_{31} = 2.87, p = .007$), and this can only be explained by information content unrelated to directional asymmetries since the mirrored hemiface provided no valid directional asymmetry information.

Directional Asymmetries

By comparing original and mirrored versions of the same hemiface (see figures 1e and 1f), we keep information other than directional asymmetries constant. Having ruled out perceptual bias as a general explanation, any differences from mirroring can be attributed to the use of directional asymmetries. There were no cases in which the mirrored hemiface produced greater accuracy than the original version of the same hemiface. We found that the original right hemiface was more accurate than the mirrored right hemiface in Agreeableness ($t_{31} = 2.59, p = .015$) and Emotional Stability ($t_{31} = 2.52, p = .017$). There was no difference in this comparison for other traits, nor was there any difference for any traits when comparing the original and mirrored left hemifaces.

Summarising Accuracy Accounts

The accuracy results can be summarised with regard to our six traits and three potential accounts as follows. Conscientiousness and Intellect/Imagination were not perceived accurately and so were not pursued further. There was no evidence to support a perceptual bias account for any trait. Both Agreeableness and Emotional Stability showed some evidence of higher accuracy for the right hemiface, and this advantage was best explained by directional asymmetries. Health showed higher right hemiface accuracy while Extraversion demonstrated a left hemiface advantage, and in both cases, evidence supported an account based on differences in information content unrelated to directional asymmetries. These results demonstrate that different traits can be represented in distinct ways between the two sides of the face.

Attractiveness

Previous studies have disagreed about which side of the face is more important for attractiveness judgements. Here we collected attractiveness ratings for different sides of the face reflecting different personality types and different levels of socially desirable traits. We suggest that

uncontrolled differences in personality expression might account for some of these previous discrepancies.

We averaged together original and mirrored hemiface ratings and then carried out analyses of variance in order to investigate attractiveness differences between the stimuli. A 2 (Composite: high or low) x 2 (Face Side: left or right) x 6 (Trait: Agreeableness, Conscientiousness, Extraversion, Emotional Stability, Intellect/Imagination, Health) ANOVA found a main effect of Composite ($F_{1, 31} = 11.97, p = .002$), such that ratings of attractiveness were higher for the more socially desirable composites. There was also a main effect of Trait ($F_{5, 155} = 5.22, p < .001$), illustrating that the composites for different traits were perceived as differently attractive.

While there was no main effect of Face Side ($F_{1, 31} = 0.31, p = .58$), there was a Trait x Face Side interaction ($F_{5, 155} = 2.73, p = .021$), such that for Conscientiousness, Emotional Stability, Openness, and Health, attractiveness ratings were numerically higher for the left than the right hemiface, while for Agreeableness and Extraversion, the right was numerically higher. This pattern of results demonstrates that whether the left or right side of the face is more attractive can depend upon the trait which is being signalled by the face. There was also a Trait x Composite interaction ($F_{5, 155} = 15.10, p < .001$). This was produced by differences in composite attractiveness for only certain traits: high Extraversion was rated as more attractive than low ($F_{1, 31} = 43.58, p < .001$), high Health was more attractive than low ($F_{1, 31} = 23.17, p < .001$), and low Intellect/Imagination was more attractive than high ($F_{1, 31} = 15.45, p < .001$). Given these results, any suggestion that one hemiface is more attractive is an oversimplification of a more complicated picture, as with the accuracy results. This may explain why previous studies have failed to agree on this issue.

We also investigated whether attractiveness ratings were associated with discrimination accuracy and socially desirable traits. In particular, we wanted to check whether individual raters might be using an “attractiveness strategy”, assigning the face they found more attractive the more socially desirable trait. This strategy cannot produce accurate discrimination unless attractive people actually have (and are not merely perceived to have) more socially desirable traits. Given the above-chance levels of accuracy we found for most traits, this account therefore does not seem likely, and attractiveness has not predicted discrimination accuracy with full faces (Kramer & Ward, 2010). However, we still thought it important to rule out this strategy if possible. We carried out regression analyses to investigate whether differences in individual participants’ ratings of attractiveness for the two composites (high minus low) for each trait and hemiface predicted their accuracy, ie did individual ratings predict subsequent discrimination? Of the six traits for the left hemiface judgements, only extraversion accuracy was significantly predicted by attractiveness

ratings ($\beta = .35, p = .049$). For the right hemifaces, only agreeableness accuracy was predicted by attractiveness ratings ($\beta = -.42, p = .018$). The negative coefficient means that those who rated the low agreeableness composite as more attractive tended to be more accurate in their judgements for this trait. This is actually in opposition to the “attractiveness strategy” above. However, neither of these results were significant after Bonferroni correction. In line with previous research (Kramer & Ward, 2010), attractiveness was unable to satisfactorily explain the accuracy of trait identification.

Discussion

Previous research has demonstrated accurate perception of certain personality and health traits from static images of the face with neutral expressions (Kramer & Ward, 2010; Little & Perrett, 2007; Penton-Voak et al., 2006). However, little is known about where in the face these signals are carried. The current research demonstrates that the two sides of the face carry different amounts and kinds of information, with Emotional Stability and Health more accurately perceived in the actor’s right side compared with the left, while Extraversion showed the opposite pattern. In addition, presenting only half the face still provides enough information for accurate perception of Agreeableness, Extraversion, Emotional Stability, and Health.

In addition, traits differed with regard to how we might best explain their hemiface differences in accuracy. Agreeableness and Emotional Stability differences were best explained by directional asymmetries, while Health and Extraversion differences suggested differing information content unrelated to directional asymmetries. By making specific comparisons, we provide a method for the investigation and separation of these accounts.

Our results apply to female faces, and we are unable to speculate how they may generalise to a male population. Previous work has found sex differences for signals from full faces (Little & Perrett, 2007; Penton-Voak et al., 2006) and this may also be the case for hemifaces. The majority of our observers were also female, and although previous research has not shown that accuracy is affected by observer sex (Little & Perrett, 2007), further investigation is needed in order to explore these issues.

The accuracy of trait identification, even from hemifaces, is striking. Our method requires participants to compare two averaged faces, high and low on a trait (see also Kramer & Ward, 2010; Little & Perrett, 2007). The averaging would be expected to increase signal-to-noise ratio (although it would remove cues from fluctuating asymmetry), and the comparison process surely helps make salient the relatively small differences between the averaged faces that account for the

differences in personality. However, even when presenting individual faces, for rating one at a time, correlations between trait values as measured by personality scales and as estimated from images of the full face can be significant (e.g., Penton-Voak et al., 2006). An interesting question for future research is whether the individual hemifaces are similarly revealing.

What might be the basis for the difference between sides in trait expression? Our stimuli contain some low-level differences between sides, as the right side is slightly more in shadow than the left due to the arrangement of lighting when the photographs were taken (see the central, full face in figure 2 for an example). However, small differences in the lighting of left and right sides do not explain our results. First, there is no simple story available that one side of the face contains more information than the other. Instead, our results were marked by an interaction such that accuracy was a joint function of the trait being judged and the side of the hemiface presented. Second, mirror reversal affected the accuracy of some traits (Agreeableness, Emotional Stability) even while holding all low-level factors constant. An interesting speculation relates to previous results on the laterality of emotional expressiveness. One explanation could be that the actor's left is more emotionally expressive (Nicholls et al., 2002) and hence more affected by transitory aspects of the situation. As such, the right side may be a more temporally stable signal of trait, as opposed to state, information. This might explain why viewers show a bias towards their left visual field when forming impressions (Burt & Perrett, 1997), and are more likely to inspect the actor's right hemiface first and for longer periods of time (Butler et al., 2005). However, this account would not explain why Extraversion was more accurately perceived in the left hemiface.

Our results also provide some evidence suggesting directional asymmetries with regard to personality expression, likely caused by observer expectations that are affected by mirrored stimuli. For example, if people unconsciously look for certain information in the right side of the face that is not present in the left, then if the right side were mirrored and so appeared to be the actor's left side, observers may treat it differently (i.e., look for information associated with the left side of the face) and perform worse. While the nature of creating composites will minimise fluctuating asymmetries, directional asymmetries will by definition still be present in our various trait groups. These may be caused by, for example, asymmetrical muscular development in the face sides due to differences in hemispheric specialisation of cognitive activity specific to those traits. Research has already demonstrated group-level asymmetries in face shape and size (e.g., Farkas & Cheung, 1981; Ferrario et al., 1995; Simmons et al., 2004), with the right side tending to be larger.

Accurate perception of traits from only half the face demonstrates that personality information is present even in this limited stimulus. It also shows accuracy remains when fluctuating asymmetry

information is removed. While previous research has shown that fluctuating asymmetry affects judgements of attractiveness (Rhodes et al., 1998) and health (Rhodes et al., 2001), there is only limited evidence suggesting that personality and facial symmetry are related (Fink et al., 2005).

Comparison with accuracy on full and internal faces (Kramer & Ward, 2010) shows that Extraversion, Emotional Stability, and Health are all signalled from full, internal, and half faces, as is Agreeableness to a more limited extent. As such, although it appears that accuracy decreases when only half the face is presented, much like when only the internal features are shown (Kramer & Ward, 2010), these same traits are signalled in all cases. Further investigation might attempt to localise information to even smaller regions, e.g., the eyes or mouth.

Our attractiveness results found that whether the left or right hemiface is more attractive can depend upon the personality trait signalled by the face. For example, this may explain why previous research has been mixed when exploring this question (Sitton et al., 2006; Zaidel et al., 1995), as studies in this field have not taken such factors as personality into account during their investigations. How individuals vary along health and personality dimensions may dictate which hemiface is perceived as more attractive. For instance, we have already shown that (accurate) perceptions of health are affected by actual levels on this trait.

In addition, analyses showed that individual perceptions of attractiveness did not account for accuracy in personality judgements. This supports previous research (Kramer & Ward, 2010) suggesting people did not base their decisions on perceptions of attractiveness.

In conclusion, we have shown that different personality and health trait signals may be lateralised, and that this in turn affects accuracy in perceptions of these traits. In addition, we have shown that some trait information relates to directional asymmetries in the face, but this account is unable to explain other differences that were found.

The next step

Evidence from this chapter and the last has demonstrated personality and health information in the full face, the internal features alone, and both hemifaces. These signals in human faces represent a system in which information is sent and received between people. Given that humans and chimpanzees have a similar evolutionary history, I hypothesised the existence of a signalling system in chimpanzees that may be similar to the one present in humans. If such a system existed in both species then signals may be sent and received by heterospecifics.

In the next chapter, I investigated this idea that humans and chimpanzees possess a similar system for signalling personality information from the face. By using chimpanzee “senders” (in the form of facial photographs) and human “receivers”, I hypothesised that personality information was present in the chimpanzee face and could be accurately perceived by humans.

CHAPTER 4: PERSONALITY SIGNALS IN THE CHIMPANZEE FACE ³

Abstract

Many aspects of personality are honestly signalled on the human face, as shown by accurate identification of personality traits from static images of unknown faces with neutral expressions. Here we begin to investigate the evolutionary history of this signal system by exploring its presence in our closest living relative, the chimpanzee. In four studies, we found that untrained human observers reliably discriminated characteristics related to extraversion solely from non-expressive facial images of chimpanzees (*Pan troglodytes*). In chimpanzees, as in humans, there is therefore information in the static, non-expressive face that signals aspects of an individual's personality. We suggest that this performance is best explained by the personalities of both species being structured in similar ways (e.g., that 'dominant' is a meaningful characteristic that encompasses behavioural biases), and also signalled through similar links between personality and facial appearance.

Introduction

Personality traits describe the stable, context-general behavioural biases of an individual organism. Factor-analytic approaches have identified a small number of human personality traits, three-factor (Eysenck & Eysenck, 1985) and five-factor models (Goldberg, 1993) being the most used. Human personality as defined by these models has cultural but also biological bases. Behaviour genetics studies estimate heritability coefficients for individual traits around .40-.60 (Bouchard & Loehlin, 2001), and human models show cross-cultural and even cross-species generalisation of personality factors (Gosling & John, 1999). In particular, humans and chimpanzees demonstrate similar, although not identical, factor structures. The most important distinction is that the factor-analytic approach identifies an additional (King & Figueredo, 1997), highly heritable (Weiss, King, & Figueredo, 2000) dominance-related factor present in chimpanzees but not humans.

Many socially-relevant traits can be accurately identified in humans solely from visible cues in the static, non-expressive face, including personality (Kramer & Ward, 2010; Little & Perrett, 2007), sociosexuality (Boothroyd, Jones, Burt, DeBruine & Perrett, 2008), trustworthiness (Stirrat

³ This research appears in publication:

Kramer, R. S. S., King, J., & Ward, R. (2011). Identifying personality from the static, nonexpressive face in humans and chimpanzees: evidence of a shared system for signaling personality. *Evolution and Human Behavior*, 32, 179-185.

& Perrett, 2010), and aggression (Carré, McCormick & Mondloch, 2009). Interpreting these results within animal signalling theory suggests a close association between the facial morphology and behaviour of the signal “sender”, and the cognitive processes for understanding the signal in the “receiver” (Maynard-Smith & Harper, 2003). Here we examine the evolutionary history of this signal system. We reasoned that if the face were part of an evolved signal system, then humans and chimpanzees might share aspects of this system. If so, some facial morphology signals should be expressed and understood between species.

The possibility of a shared signal system is plausible in part due to evidence from comparative studies showing similarities in face processing for the two species, including homologous specialised brain regions (Parr, Hecht, Barks, Preuss & Votaw, 2009), cross-species identification of relatedness (Alvergne et al., 2009), sensitivity to facial configurations (Parr, Heintz & Akamagwuna, 2006), and homologies in expression (Parr, Waller, Vick & Bard, 2007). However, a shared signal system of personality would require a variety of other physical and psychological homologies, including behavioural biases as reflected by aspects of personality structure, facial morphology, and the cognitive means for correctly interpreting and using these signals from the face.

To test the possibility of a shared signal system, we measured the ability of humans to understand signals from the static chimpanzee face, related to extraversion. Our focus on extraversion was motivated by previous findings. First, in the human face, the signal for extraversion is strong, and apparent in both individual (Penton-Voak, Pound, Little & Perrett, 2006) and composite faces (Kramer & Ward, 2010). Second, personality characteristics related to human extraversion, such as individual differences in dominance, sociability, and activity levels, are widespread in non-human animals (Gosling & John, 1999), including other primates (e.g. chimpanzees; King & Figueredo, 1997), other mammals (e.g. hyenas; Gosling, 1998), fish (e.g. guppies; Budaev, 1997), and even invertebrates (e.g. octopuses; Mather & Anderson, 1993). Finally, the characteristic of ‘dominant’ is encompassed by the trait of Extraversion in the human taxonomy (Goldberg, 1990), and is a particularly robust measure in chimpanzees, demonstrating the single highest factor weighting of any characteristic in the chimpanzee personality model (King & Figueredo, 1997), and both reliability (Freeman & Gosling, 2010), and external validity in predicting individual behaviour (Pederson, King & Landau, 2005). We carried out a series of four studies in order to investigate accuracy in identifying characteristics relating to extraversion from static chimpanzee faces.

Study 1: accurate personality identification from the chimpanzee face

The first study determined whether people could accurately perceive characteristics relating to extraversion and other personality traits from chimpanzee facial photographs using a forced-choice methodology.

Method

Participants

Forty-three students from Bangor University (age 19-50 years, 26 female) took part in exchange for course credit.

Stimuli

We obtained an initial set of 37 photographs of chimpanzees, each with previously collected personality information as described by King and Figueredo (1997). The photographs were mostly full body images and showed the chimpanzees in a natural setting. Chimpanzees were either looking straight at the camera or in three-quarter view, and the images were mirrored as necessary so that all angled to their left. All images were cropped to show only the head, with a small amount of neck/body and background remaining (Fig. 1A). We selected the images without valenced facial expressions, e.g. without teeth visible or strong shadowing over the eyes. Images were approximately 300 x 300 pixels in size, or about an 8.5 cm square on the screen.

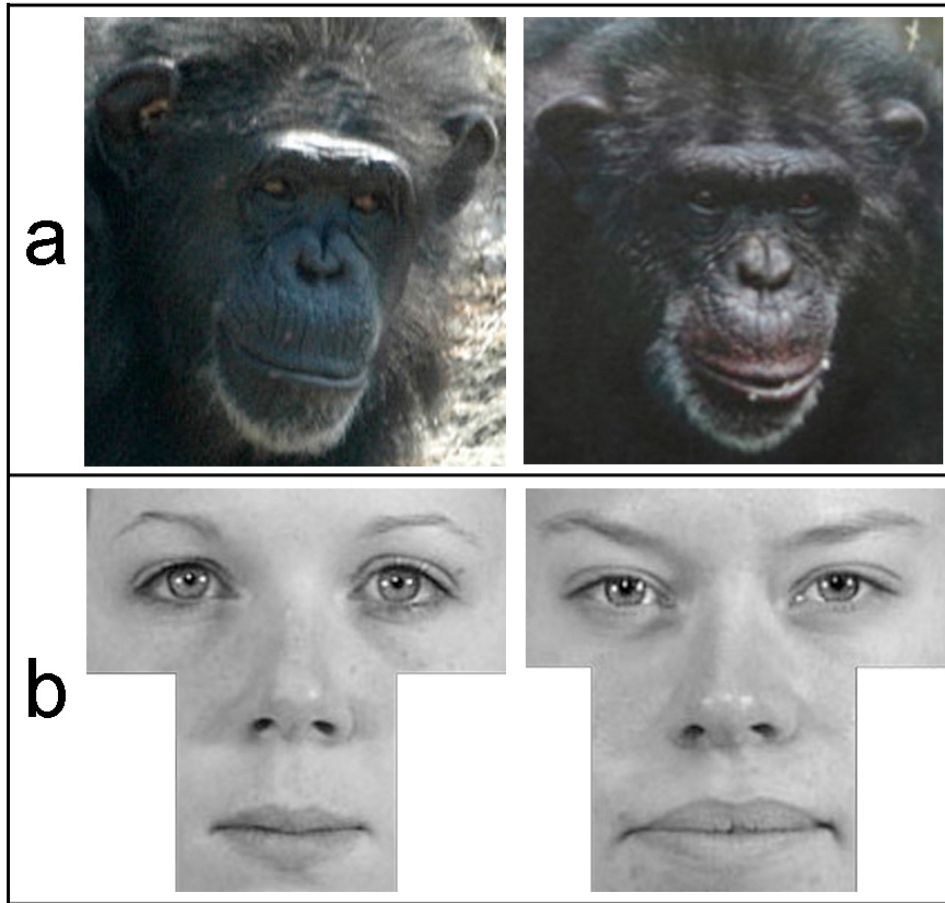


Figure 1. Examples of honest signals of personality. (A) Individual images of two female chimpanzees scoring low (left) and high (right) on dominance, a characteristic that maps onto human Extraversion (70% of participants accurately identified this specific pair). (B) Examples of stimuli from Study 4: individual face images, with external features removed, of two women scoring low (left) and high (right) on the Extraversion scale (67% accuracy on this specific pair).

We selected 15 of the 43 characteristics assessed in the King and Figueredo (1997) database. These characteristics were chosen in order to represent the six chimpanzee personality factors (King & Figueredo, 1997): the two characteristics with the highest loading on the five traits most closely related to the human Big Five, and the five characteristics with the highest loading on the chimpanzee-specific factor of Dominance. The characteristics chosen were “inventive”, “inquisitive”, “unemotional”, “excitable”, “sympathetic”, “sensitive”, “reckless”, “erratic”, “sociable”, “active”, “dominant”, “dependent”, “fearful”, “decisive”, and “timid”. For each characteristic, the five highest and five lowest-scoring chimpanzees were selected. In the end, we had 30 different chimpanzee images.

Procedure

A Latin-square design was used to create five sets of high-low image pairs for each characteristic, such that within a set each high and each low image appeared once (producing five pairs), and across all sets, each low-scoring image for a characteristic was paired with each high-scoring one. The presentation of the high stimulus on the left versus the right of the screen was randomly decided for each trial. For each participant, pairs and characteristics were presented in random order. Participant numbers within each set were balanced as much as possible.

A single trial proceeded as follows. Participants were shown a high/low pair and asked to choose the face best fitting an on-screen definition of a personality characteristic, e.g. “more dominant: more able to displace, threaten, or take food from others, or more likely to express high status by decisively intervening in social interactions” (King & Figueredo, 1997). The image pair and definition were provided onscreen throughout the trial. Responses were made by clicking the chosen face and were not speeded.

After the forced choice trials, participants were shown each chimpanzee photograph used in the prior trials on the computer screen, one at a time, and instructed to rate how old they thought the chimpanzees were on a scale of 1 (young) to 5 (old).

Participants also completed a task involving human faces that will not be included in the present work. The chimpanzee and human trials were blocked separately and the order of the two blocks was counterbalanced across participants. Blocking order had no significant effect on 14 of the 15 characteristic, all $ps > .224$, but did affect performance on the characteristic of ‘unemotional’, $t_{41} = 2.34$, $p = .024$. As indicated below, overall performance on this characteristic was no different from chance, and we did not pursue this effect further.

Results and discussion

Identification accuracy was calculated for each characteristic. All significant findings were related to characteristics loading on human Extraversion. We found accurate performance on the characteristic of ‘dominant’: accuracy = 0.59; $t_{42} = 3.01$, $p = .004$, and also ‘active’: accuracy = 0.72; $t_{42} = 6.76$, $p < .001$. Interestingly, perception of the characteristic ‘sociable’ was significantly worse than chance: accuracy = 0.36; $t_{42} = -4.37$, $p < .0001$, suggesting that information was accurately perceived but systematically misinterpreted. In addition, accuracy on ‘sympathetic’ (which loads onto human Agreeableness) was close to significant: accuracy = 0.56;

$t_{42} = 1.84, p = .073$. These results demonstrate that some characteristics relating to Extraversion, and possibly Agreeableness, are accurately perceived in chimpanzee faces.

Participants were also able to accurately estimate chimpanzee age, as age at the time of their rating by zoo keepers was correlated with perceived age as judged by participants, $r_{28} = 0.69, p < .001$. We examine effects of age further in Study 2.

Study 2: accurate identification of dominance in single chimpanzee faces

This study focused more specifically on characteristics relating to Extraversion and Agreeableness, as motivated by the results of Study 1. We used a ratings task in order to incorporate more stimuli and generalise our findings beyond one type of methodology. Single chimpanzee faces were presented and rated for different characteristics. Instead of measuring discrimination accuracy, we measured the strength of correlation between real and perceived characteristics.

Method

Participants

A different set of 30 students from Bangor University (age 18-27 years, 20 female) took part in exchange for course credit.

Stimuli

The same images were used as in Study 1. However, we replaced the image of one chimpanzee with a more extreme personality value for one with a more closed mouth but a less extreme personality value.

Procedure

Participants were shown each image on the computer screen, one at a time, and instructed to rate them on a scale from 1 (very low) to 7 (very high). The stimuli were rated on the four characteristics identified in Study 1: sociable, active, dominant, and sympathetic. A description of each characteristic appeared onscreen while that rating was being made. The characteristics were

blocked separately, and order of block presentation was counterbalanced between participants. Trials appeared in randomised order for each participant.

Participants also completed a task involving human faces that will not be included in the present work. The chimpanzee and human trials were blocked separately and the order of these two blocks was counterbalanced across participants. We verified that the order of the blocks did not affect performance on any of the chimpanzee judgements, all $ps > .05$.

Results and discussion

We calculated the mean rating for each chimpanzee for each characteristic. We then correlated these mean ratings with actual values of chimpanzee characteristics (degrees of freedom therefore reflect the number of chimpanzees judged). Ratings of dominance significantly correlated with actual dominance, $r_{28} = 0.42$, $p = .022$. The interrater reliability of dominance ratings as determined by Cronbach's α was .93. Pairwise correlations of perceived and actual values for other characteristics were not significant, all $ps > .32$. The characteristic of dominance could therefore be accurately assessed, even when participants were unable to directly compare the faces associated with extreme personality values.

Accuracy in dominance ratings did not appear to be affected by age-related cues. Estimates of the ages of individual chimpanzee images (obtained in Study 1) were not correlated with estimates of dominance for those same individual images, $r_{27} = -0.17$, $p = .380$. Furthermore, the chimpanzees' actual ages were not correlated with actual dominance, $r_{29} = 0.01$, $p = .964$, meaning that age was in any case not a valid cue for dominance with this group.

We also considered whether dominance ratings might be influenced by implicit sex identification. If male and female chimpanzees differ in dominance, and participants were able to pick up on this cue consciously or otherwise, then accuracy on this task may reflect an implicit ability to identify chimpanzee sex rather than dominance. To see whether this was likely, we compared the actual dominance of males to females in our test set, but these did not significantly differ, $t_{28} = 1.48$, $p = .149$ (although such differences have been reported in other chimpanzee data sets, e.g. Dutton, 2008; King, Weiss & Sisco, 2008). Likewise the perceived dominance of the two sexes was not significantly different, $t_{28} = 0.24$, $p = .811$. It therefore seems unlikely that people were making their judgements on sex rather than dominance. However, in the next study we tested this possibility directly.

Study 3: within-sex discrimination of dominance

Here we asked whether people could accurately distinguish levels of dominance within a single-sex group. We presented images of male and female chimpanzees in separate blocks and used forced-choice discrimination to assess accuracy of dominance perception.

Method

Participants

A different set of 30 students from Bangor University (age 18-34 years, 22 female) volunteered to participate.

Stimuli

From the 30 chimpanzees used in Study 2, three were removed to produce a more controlled set. These included two chimpanzees who had visible facial injuries and one photograph of relatively low image quality. From the remaining 27 chimpanzees (12 females, 15 males), the highest and lowest four male and female chimpanzees for the 'dominance' characteristic were selected. Images were approximately 300 x 300 pixels in size, or about an 8.5cm square on the screen.

Procedure

Similar to Study 1, high/low pairs of chimpanzee faces were presented onscreen and participants were instructed to select the more dominant one. A definition of 'dominant' was also provided onscreen throughout. Each 'low dominance' face was paired with every 'high dominance' face of the same sex, producing 16 male and 16 female pairs. The position of each 'high' face was counterbalanced for side of presentation for each participant. The trials were blocked by stimulus sex, with the order of the pairs randomised within blocks for each participant, and the order of the two blocks counterbalanced between participants.

Results and discussion

Identification accuracy was calculated for each characteristic. Accuracy was significantly above chance when participants were asked to make within-sex comparisons, both for male chimpanzees: accuracy = 0.70; $t_{29} = 6.00$, $p < .001$, and for female chimpanzees: accuracy = 0.60; $t_{29} = 3.82$, $p < .001$. In addition, participants were more accurate with male than female chimpanzees, $t_{29} = 2.48$, $p = .019$.

We can therefore be confident that dominance accuracy is present for both male and female chimpanzees. Combined with previous research on human faces (Penton-Voak et al., 2006), we can see that there is some accuracy in characteristics relating to extraversion for both human and chimpanzee faces. Our final study investigated whether accuracy on these two tasks was related.

Study 4: comparing accuracy from human and chimpanzee faces

Using forced-choice discrimination, we explored accuracy on chimpanzee dominance and human extraversion in order to see whether performances with these two types of stimuli were related.

Method

Participants

A different set of 36 students (age 18-27 years, 26 female) from Bangor University took part in exchange for course credit. Participants completed measures of personality (Donnellan, Oswald, Baird & Lucas, 2006), empathy (Davis, 1980), and autism (Baron-Cohen, Wheelwright, Skinner, Martin & Clubley, 2001).

Stimuli

In this study, high/low pairs were created for both chimpanzee and human faces. For the chimpanzees, the set of 27 images from Study 3 were used, and the five chimpanzees scoring highest and lowest on dominance were selected, without regard to sex. For the human discrimination, 36 Caucasian females (see Kramer & Ward, 2010, for details) were photographed

under standard lighting conditions with neutral facial expressions. All jewellery and make-up were removed. Images were cropped to show only the internal facial features, and were converted to black and white (Fig. 1B). These students completed a Big Five personality assessment (Donnellan et al., 2006), and were then sorted for Extraversion, with the highest and lowest five being selected, subject to the constraint that scores on other traits were equivalent. This allowed us to maintain differences between the two sets for Extraversion but minimise other trait differences that may interfere with signal reading. Images were approximately 275 x 250 pixels in size, or about 8 x 7 cm on the screen.

Procedure

Discrimination of human and chimpanzee pairs were made in separate blocks, presented in counterbalanced order between participants. In the chimpanzee blocks, pairs of chimpanzee faces were presented onscreen and participants were instructed to select the more dominant. Each 'low dominance' face was paired with each 'high dominance' face, producing 25 pairs. The position of each 'high' face was counterbalanced for side of presentation for all participants, with each participant seeing each face on one side three times and on the other side twice.

The procedure used with the human faces was identical, although participants were instructed to select the more extraverted. A definition of 'Extraversion' was also provided onscreen throughout: "more talkative, energetic, social, assertive".

Results and discussion

As expected from our previous studies, identification accuracy was again significantly above chance for chimpanzee dominance: accuracy = 0.58; $t_{35} = 3.24$, $p = .003$. Performance was also accurate on human Extraversion judgements: accuracy = 0.77; $t_{35} = 10.34$, $p < .001$. However, the within-rater correlation for accuracy on chimpanzee and human faces was not significant, $r_{34} = -0.08$, $p = .65$. We also saw some individual differences in performance on the tasks. Participant scores on the 'social skills' domain of the Autism Spectrum Quotient were negatively correlated with accuracy on the human discrimination task, $r_{34} = -.37$, $p = .025$, but not the chimpanzee task, $r_{34} = -.01$, $p = .972$. This negative relationship suggests that those with higher levels of autistic-like traits relating to social skills were specifically worse at reading the signs of extraversion in human faces.

In addition, chimpanzee accuracy was correlated with participants' conscientiousness scores, $r_{34} = .44, p = .007$. While one could imagine that trying harder on this task may lead to improved accuracy, this does not explain the lack of correlation with human accuracy.

General discussion

The results of these four studies demonstrate that humans can accurately perceive characteristics relating to extraversion in chimpanzee faces on the basis of static, non-expressive cues. In particular, people can use cues in both the human and chimpanzee face to identify individuals who are biased towards social activity and dominance-related behaviours.

The ability to detect the characteristic of dominance was an especially robust finding, and it is worth being clear about the nature of this characteristic. The term "dominance" is often used to refer to a situation-specific construct that describes the relationship between individuals and the organisation of the social hierarchy within the group. However, "dominance" as discussed here refers to the broad personality characteristic relating to the chimpanzee's overall competitive tendency or prowess. This characteristic is heritable (Weiss et al., 2000) and reflects a disposition that is relatively stable over time and context. We would expect that these two types of dominance are positively correlated (de Waal, 2000); however, to be clear, it was the personality characteristic, not status per se, that was accurately identified in our studies.

How can we best explain the performance of human observers in accurately decoding the personalities of chimpanzees from their static face images? Clearly there is relevant information present in the chimpanzee face, but why would humans be able to accurately process this information? Particularly when, as in our case, these humans have no prior experience of chimpanzees? We hypothesise a shared system for signalling personality from the face in humans and chimpanzees, that is, on the basis of their shared evolutionary past, chimpanzees and humans share aspects of a system for communicating behavioural biases to conspecifics.

One might argue that because both humans and chimpanzees have similar social environments, facial structures, and so on, the two species could have separately developed signals of personality from the face. Rather than a shared system due to common ancestry (homology), the two species may have similar signal systems because they both solved similar adaptive problems (analogy). However, I argue that this does not explain the evidence that signals were accurately perceived across species. As an example, unless we hypothesise that dominance can only be

signalled from the face in one way irrespective of species, the fact that it is signalled similarly in both humans and chimpanzees supports the idea of a homologous system.

A shared signal system would implicate a variety of physical and psychological systems. These would include (1) shared aspects of personality; (2) shared links between personality and facial morphology; and (3) shared cognitive mechanisms for processing those links. We have already discussed the first point, and the substantive overlap in human and chimpanzee models of personality, as well as the heritability and external validity of chimpanzee personality models to predict behaviour (Pederson et al., 2005; Weiss et al., 2000). Our present results, demonstrating that people are able to identify links between personality and facial morphology in both humans and in chimpanzees, argues strongly for the second point. The point which is not yet demonstrated is the third. Our results show that humans have the cognitive means for processing at least some of the available signals in the face and their associations with personality. However, it is not yet known whether chimpanzees have a similar ability to process and use these signals.

We predict that chimpanzees will be able to identify such signals, at least in the chimpanzee face. Our reasoning is as follows. It is clear that chimpanzees inhabit complex social structures. It is also clear that information in the chimpanzee face, along with associated cognitive abilities, allows chimpanzees to identify important social traits in their conspecifics, such as relatedness and emotional expressions. This information is no doubt used to facilitate social interaction. Given these well-agreed facts, and given our present results, demonstrating there are signals relating to extraversion in the chimpanzee face, it would be a surprising evolutionary blindspot if the chimpanzee species were simply unable to process this other type of useful information on their faces. It would be more surprising still that untrained humans *were* able to use this same information from chimpanzees. We therefore predict that chimpanzees will be able to use the signals that are evidently available from their conspecifics. This evidence, if found, would be a crucial foundation for the more general hypothesis of a homologous signal system.

As we reviewed in the introduction, characteristics related to extraversion approximate a universal form of individual difference. These characteristics are widely distributed across mammalian as well as non-mammalian taxa. Extraversion in both humans and chimpanzees is heritable and displays both internal and external validity. The fact that dominance was readily communicated between species suggests the importance of this characteristic in both human and chimpanzee social structures. Indeed, both chimpanzee dominance (King & Landau, 2003) and human extraversion (Costa & McCrae, 1980) are correlated with subjective well-being. There are of course also important differences in these personality structures, for example as reflected in the six-

factor chimpanzee and five-factor human models. These differences may account for some of the errors in cross-species identification.

Our findings also support previous studies measuring signals of trait extraversion from individual human faces (Penton-Voak et al., 2006), that have shown mixed results (Shevlin, Walker, Davies, Banyard & Lewis, 2003). In addition, while internal features alone have been shown to allow accuracy with composite images (Kramer & Ward, 2010), our results are the first to demonstrate this with individual photographs, thus demonstrating that the signal for extraversion in individual images is still present when information from jawline and skin colour are removed.

From previous studies, it has also been an open question whether accurate personality identification from the human face is based upon the heritable or the acquired components of personality (Kramer & Ward, 2010; Little & Perrett, 2007). The fact that humans can identify such signals in chimpanzees clearly indicates some degree of signal which is not specific to any human culture. However, the lack of correlation between accuracy with human and chimpanzee faces in our final study suggests that cultural learning also plays a role. Our participants had little or no experience with the behaviours and faces of any individual chimpanzees, and therefore little room for individual differences in that experience. However, when judging human faces, we would expect people to have a wide range of individual differences in experience which could affect their performance. For example, extraverts demonstrate better visual memory for faces than introverts (Li, Tian, Fang, Xu, Li & Liu, 2010). Under these assumptions, we might then expect little correlation in performance on human and chimpanzee tasks, for what are essentially statistical reasons.

However, our results still point to some more uniquely human signal in the face. We found in our final study that individual differences in Autism Spectrum Quotient (AQ) measures were correlated with the ability to identify traits in human, but not chimpanzee, faces. As autism is associated with a variety of behavioural deficits in face processing, and specific neurophysiological irregularities (Dawson, Webb, & McPartland, 2005), an interesting question is whether high-scoring AQ individuals may have social problems relating to difficulties in reading the non-verbal behavioural signals tested in our studies. In any case, while our overall results argue for commonalities between human and chimpanzee signal systems, the fact that AQ predicts accuracy on human but not chimpanzee faces also demonstrates some dissociation. This may also be explained in terms of AQ scores affecting the reading of extraversion signals but not those of dominance. However, further research is needed in order to clarify this issue.

Finally, adaptive theories of animal signalling argue that the system is unlikely to be stable unless there is a net advantage to both the sender and the receiver in honest communication (e.g. Krebs & Dawkins, 1984). It is easy to imagine benefits for the receiver in predicting the personality and subsequent likely behaviours of others. Research has shown that both humans (Jones et al., 2010) and rhesus monkeys (Shepherd, Deaner, & Platt, 2006) are affected by social status and dominance as reflected in the face during a gaze-cuing task. More interesting is to ask what benefits there may be for the signal sender in this arrangement. While there might be some advantage in concealing likely behaviours and intentions, interpreting our results within a framework of adaptive signalling suggests that in human and chimpanzee social structures, there are also advantages in displaying those behaviours, or at least large costs for concealing them. In conclusion, these four studies provide the first evidence of an honest signal system for personality attributes across species, with evolutionary origins dating back at least to the last common ancestor of chimpanzees and humans.

CHAPTER 5: GENERAL DISCUSSION

In this section of the thesis, I readdress several issues in light of the findings presented in the three research chapters.

Accuracy in trait perceptions

If we consider these three chapters together, we can start to understand which traits can and cannot be read from the face. In Chapter 2, full-face composites of females provided information that produced accurate perceptions of agreeableness, extraversion, neuroticism, and physical health. Presenting only the internal facial features in greyscale led to accuracy in these same four traits (with the addition of intellect/imagination). Although accuracy differed across hemifaces (Chapter 3), we basically found these same traits were read in one or both sides of the face. As such, we can be confident of the reliability of our findings with regard to which traits were signalled.

However, all our results were produced using variations of the same stimulus images, i.e., the initial composites of fifteen women were cropped or altered in some way to produce the stimuli and subsequent results for the internal faces and hemifaces. As such, might our findings be specific to idiosyncrasies in our images? We believe that this is unlikely since each image is a composite of fifteen faces. By using high and low composites, we are using information from thirty participants, and the number of faces represented across all the different traits is even greater. In addition, our results seem in good agreement with the completely different set of composites used in previous research, which found accuracy in females for agreeableness and extraversion (Little & Perrett, 2007), as well as conscientiousness and neuroticism (Little & Perrett, 2007; Penton-Voak et al., 2006). (Physical health was not investigated in these articles).

Recently, we have also investigated personality accuracy in three-dimensional facial composites (Jones, Kramer, & Ward, in press). We collected a new database of actor photographs from which we constructed our stimuli, and we created composites based upon self-report scores using a different questionnaire measure to our previous work (Big Five Inventory; John & Srivastava, 1999). In addition, the image delineation (the placement of landmarks at specific points on the faces) was done by a different researcher, and the morphing techniques used also differed from our two-dimensional faces. Even so, the results were remarkably similar to our previous findings - accuracy for perceptions of agreeableness, neuroticism, and physical health. In addition,

the right side of the face was again found to signal more information regarding personality and health when compared with the left side.

Further, our findings of accuracy with individual female faces for extraversion replicate those of Penton-Voak and colleagues (2006), who used a different set of faces to ours. Therefore, we see our findings as an extension of previous work, while demonstrating a replicability that argues firmly against any explanation based on image idiosyncrasies.

Causes of the personality-face relationship

Having established a link between personality and facial appearance, I return to the nature of this relationship. What mechanisms might explain this link? First, Chapter 2 provided evidence that the internal facial features still conveyed personality information in the face when external features were removed. This may support the argument that sex hormones play only a minor role if any in the relationship between personality and facial appearance, given that their effects seem predominantly to manifest themselves facially in this external region.

Androgens like testosterone are thought to stimulate growth of the facial bones, including the brow ridge and lower jaw (Tanner, 1978), although direct evidence of this relationship is lacking. While there is limited evidence that higher levels of circulating testosterone correlate with more masculine faces (Penton-Voak & Chen, 2004), there is likely an indirect relationship between testosterone and facial growth. In contrast with testosterone, oestrogen is thought to stop bone growth, causing a smaller lower face, and may additionally lead to increased fullness of the lips, assuming they parallel fat deposits found elsewhere in the female body that are caused by oestrogen levels (Johnston & Franklin, 1993). Indeed, women with higher levels of late follicular oestrogen have more feminine faces (Law Smith et al., 2006).

Given the likely effects of sex hormones on facial bone growth, in particular on the shape of the external regions, our results with internal facial features in females could suggest minimal effects of these hormones since most of the lower face, along with various relative measures of height/width that raters may use, is not visible to influence judgement. Despite these missing features, we found no detriment in the accuracy of perceptions for agreeableness and neuroticism. However, extraversion and physical health perceptions decreased in accuracy when the external features were removed, suggesting that such features may play a role in their signalling. Complicating matters, we found that these two traits also showed the strongest link with attractiveness, with the high-scoring composite images rated as significantly more attractive than

the low composites for both full faces and internal features only. Therefore, we are currently unable to separate out potential effects due to sex hormones, and their link with facial development and subsequent consequences on attractiveness.

We might also cast doubt on explanations whereby certain personalities lead to certain facial expressions, and these become etched into our faces over time and/or simply readily adopted during photography sessions. Our results with hemifaces (Chapter 3) demonstrated that the actor's right side carries more information with regard to personality and health. This is in contrast with a significant body of research showing that the actor's left hemiface is strongly linked with emotional expressions. As such, we hypothesise that the right hemiface informs with regard to more stable, context-general behavioural biases, and this may be distinctive from information signalled through facial expressions. Interestingly, we might also consider this hemiface distinction as a difference in signalling static versus dynamic information, given that everyday expressions contain a temporal component. If our investigations were successful in identifying specific facial measurements and other relationships that were associated with personality independently of any temporary facial changes due to expression, we could more forcefully support this idea that facial layout itself is the signal that our judges are utilising.

Our results also argue against the idea that knowledge relating facial structure and personality is solely acquired. It seems unlikely that experience and learning during our lifetimes can fully explain the link between facial appearance and behaviour when we find cross-species accuracy in identifying personality from the face (Chapter 4). That chimpanzees also possess a similar relationship between facial structure and personality, and that this relationship led to accuracy in human observers, provides strong evidence for an evolved system that dates back to a common ancestor. That both species demonstrate such a similar personality-face relationship for dominance, for example, cannot be satisfactorily explained by the idea that the relationships between facial appearance and personality separately evolved in the two species. Simply, why would the signal for dominance in the faces of both species take on the same form via separate evolutionary pathways? Related, if people acquire knowledge linking face and personality through experience, this could not explain why these same links are apparent, and accurately perceived, in another species. However, for the moment, we only show evidence for certain traits in the face across species (predominantly relating to extraversion and dominance), perhaps suggesting that some signals may be unique to humans and potentially acquired rather than the product of a common ancestor. In addition, we are yet to find a relationship between signal-reading abilities across species, which we might predict if the same signals were present in both us and chimpanzees. In summary, we argue

for a face-personality relationship in terms of an inherited ability to identify personality information from related facial properties. However, further research is needed in order to determine whether this signalling system incorporates all, or only certain, socially-relevant traits.

Further, I suggest a significant role for genetics in the personality-face relationship itself. Research estimates heritability coefficients for individual personality traits to be 0.40–0.60 (Bouchard & Loehlin, 2001), while facial measurements appear to be similarly heritable. For example, researchers demonstrated heritability estimates ranging from 0.46 for nose height, to 0.72 for the distance between the outside of the eyes (Jelenkovic, Poveda, Susanne, & Rebato, 2010). As such, it is not difficult to imagine a link between both inherited personality and facial characteristics.

Attractiveness

As I discussed in Chapter 1, attractiveness causes a perceptual halo whereby those seen as attractive are judged to have socially desirable traits. Further, there is some evidence demonstrating that attractiveness is related to physical fitness (Hönekopp, Bartholomé, & Jansen, 2004), physical health (Shackelford & Larsen, 1999), and athletic flair (Park, Buunk, & Wieling, 2007). However, if attractiveness is going to account for accuracy in perceiving personality and health, then those who are judged to be more attractive must actually possess more socially desirable traits. Comparing high and low composites in our studies (Chapters 2 and 3), we found evidence that more extraverted and more healthy females were also more attractive. Therefore, attractiveness may have served as a useful cue when judging these two traits. However, investigating individual judgements (Chapter 2) provided no evidence that participants used their perceptions of attractiveness when judging extraversion and health. Further, for other personality traits, attractiveness could not explain the accuracy that we found. Of course, with our chimpanzee results in Chapter 4, characteristics relating to extraversion were accurately perceived in the face, while attractiveness played no role.

Taken together, our research and the literature investigating attractiveness as an ornament of quality can be seen as complementary rather than contradictory. Attractiveness may represent a single cue to fitness, quality, and so on, and this leads to a redundancy in the signal across multiple modalities (e.g., Saxton, Burriss, Murray, Rowland, & Roberts, 2009). In addition, personality variation between individuals may be signalled in the face separately from overall genetic quality. This is because personality profiles are differently attractive to different potential partners, as are the faces that signal them (Little, Burt, & Perrett, 2006). There is likely no single combination of

trait values that is optimal in an environment where each one may represent a trade-off between fitness costs and benefits (Nettle, 2006). Therefore, while it seems reasonable that high levels of genetic fitness will be regarded as universally attractive, there are no ideal personality scores when considering the population as a whole, rather than the individual.

Women's and men's faces

The experiments in these chapters investigate signals from chimpanzees of both sexes, but only female faces in humans. Our main reason for this is one of practicality: it is easier to obtain usable photographs of women's faces. There are fewer male undergraduates in our psychology department, and even when we conduct university-wide photography sessions, many male photographs are unusable due to the presence of facial hair. This obscures the face and also affects perceptions (Neave & Shields, 2008) in both individual photographs and composite images.

Previous research using male composite images found mixed results. Fewer traits appeared to be signalled from the male face in comparison with females in one previous article (Little & Perrett, 2007) but not another (Penton-Voak et al., 2006). As such, results with male facial signals of personality appear to be less replicable. This issue would be an interesting one to pursue using samples of females and males who express equivalent ranges on the Big Five traits.

Individual differences in accuracy

Throughout our research, we have attempted to identify individual differences in accurately perceiving traits from the face. Intuitively, we might hypothesise that the personality profile of the judge/rater would influence their ability to read the personalities of others, e.g., high extravert judges might be better able to identify high extravert actors. However, so far, we have found no evidence supporting this idea.

The only significant results regarding individual differences in rater accuracy relate to autism (Chapter 4). We found that judges who scored higher on the "social skills" domain of the Autism Spectrum Quotient (AQ) performed worse on a discrimination task involving the identification of extraversion in human faces. This suggested that those with higher levels of autistic-like traits relating to social skills were specifically worse at reading the signs of extraversion. This makes some intuitive sense, given that people with poor social skills (and perhaps a resulting lack of social experience) might fail to recognise a sociable and outgoing quality in others. Indeed, there is some

evidence, at least in autistic children, that a preference for looking at people first in a scene is correlated with the ability to recognise faces (Wilson, Brock, & Palermo, 2010). However, the inverse relationship may be true, whereby the inability to read signals regarding extraversion may produce negative social experiences and result in poor social skills.

Another source of variation in perceiver accuracy may relate to individual differences in taste with regard to attractiveness. People find more attractive the faces of those who appear to display the personality traits they specifically look for in a mate (Little et al., 2006). As such, we might predict that these preference differences may also influence individual differences in the accuracy of perceptions. For example, if my ideal partner were highly agreeable, this may mean that I am better at picking up on this trait in the faces of others since I find the quality attractive and it is something that I am seeking. Therefore, further research would do well to investigate whether personal preferences might explain at least some of the variation in individual ability to read personality from the face.

Signals reconsidered

In Chapter 1, I outlined the difference between cues and signals, and explained why information in the static face might be considered a signal rather than just a cue. With the results of our research, we may again address this issue. Is the face merely a source of information, or has it evolved because of its effect on others? Our research, combined with the findings of numerous other groups, has now established the static, non-expressive face as a source of useful social information. Further, we know that unfamiliar others can accurately receive this information, allowing them to predict the behaviour of these senders.

We can add to this discussion the knowledge that the face has undergone a great deal of change since the last common ancestor that humans shared with chimpanzees. Humans and chimpanzees have significant craniofacial differences from birth, with ontogenetic trajectories in growth following conserved and somewhat parallel pathways (Ackermann, 2005). However, there is evidence demonstrating that postnatal growth differs both quantitatively and qualitatively between species. Human facial development involves more of a vertical translation of the midface, while in chimpanzees, midface changes were defined by a downward rotation (Bastir & Rosas, 2004). As such, since the chimpanzee-human divergence around six million years ago (Kumar, Filipski, Swarna, Walker, & Blair Hedges, 2005), the human face has undergone significant changes.

Even within humans, facial morphologies (possibly even prenatally) are distinctive over different populations, as are the ontogenetic trajectories of craniofacial growth across these populations (Strand Viðarsdóttir, O'Higgins, & Stringer, 2002). Research therefore suggests that the human face is highly configurable during development.

Despite these major changes to the human (and chimpanzee) face over evolutionary time since our last common ancestor with chimpanzees, we still find that similar signals of personality have been preserved in both species. As such, we argue that at the very least, evolutionary pressures have maintained these facial differences in different personality types regardless of significant changes in the face.

Having established the existence of signals in the human face that are received by others, one might then reasonably question why such signals have evolved to be present. It is easy to imagine why receivers may benefit from accurate information about senders, since one would presume that any extra information about an unfamiliar interaction partner would only help the receiver in achieving their goals. However, benefiting the receiver does not explain why the signal sender has evolved to send out information. If sending information was disadvantageous for the sender, evolution would have produced senders who did not signal, or sent deceptive messages. In return, the receiver would subsequently learn to ignore these signals if sent. Since this is not the case, the sender must benefit from sending by definition. One possibility is that these facial signals of personality aid the search for suitable mates. Individual differences in personality lead to corresponding differences in the personalities of our ideal partners. Support for this idea comes from evidence demonstrating that people who value particular personality traits in a potential partner will also find more attractive those faces that appear to display those traits (Little et al., 2006). This may explain why attractiveness perceptions are equally influenced by the shared tastes of a population and the private tastes of an individual (Hönekopp, 2006). As a result of these individual preferences, it makes sense that both the sender and receiver will benefit from signalling personality information since finding a suitable mate will be that much easier.

A shared signalling system

Our results in Chapter 4 demonstrate that the chimpanzee face contains personality information, and that humans can accurately perceive this information. 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. 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 & 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 signalled from the face, unless this information is signalled 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 signals. Third, being able to predict the stable behavioural biases of other group members - that is, their personalities - seems like a useful social advantage. So the personality signals are valuable. However, further research is needed to determine whether and how chimpanzees might use these potential signals to the behaviour of their conspecifics.

Implications and future research

Considered as a single research programme, these research chapters make significant progress in establishing the location and nature of signals in the face. While previous research had demonstrated initial evidence of a link between facial appearance and personality, it still remains an important question as to how the face conveys information that leads to accurate perceptions. There is certainly scope for more in-depth investigation into this relationship. For example, if we were to find correlations between personality scores and specific facial measurements, e.g., more extraverted individuals had a proportionately wider mouth, then we could investigate whether these sources of information are the ones that raters are using. One could also imagine training artificial neural networks to predict human personality from facial photographs alone, in the same way that they are currently able to identify an individual's sex (e.g., Tamura, Kawai, & Mitsumoto, 1996). Recent research has already demonstrated that computers can learn to predict human perceptions of various traits from the face (Rojas, Masip, Todorov, & Vitria, 2011), and so predicting actual actor trait scores seems plausible.

Further, it would be interesting to begin teasing apart the different accounts (see earlier) of how personality and facial appearance are related. Using the above example, if extraverts did have wider mouths, we could try to understand the cause-effect relationship for these two characteristics.

Perhaps a genetic or hormonal underpinning explains both features, either through inherited characteristics from our parents, or through specific hormone levels during pubertal development. Alternatively, we may tend to assume that those with wider mouths are more outgoing, and as a result, we interact with them in ways that cause them to become more extraverted over time. However, for this to be true, we would still need to explain the origin of this ‘extraverts have wider mouths’ assumption. As another alternative, perhaps extraverted people behave in ways that influence the shape and size of their mouths over time, e.g., they may talk and smile more often than introverts. Once we can identify what it is about the face that signals personality information, we can generate contrasting hypotheses that experimentally test these accounts in order to differentiate the contributions that they might make.

Again related to the nature of the information, we have mostly used composite images when investigating signals of personality and health in the face. As I mentioned earlier, it seems intuitive that these would serve to make identification of high versus low scorers on any trait clearer because the signal-to-noise ratio is increased. Group differences should be maintained while individual idiosyncrasies will be minimised. However, there has been no experimental test of this idea to date. The untested assumption is that everyone signals traits in the same way. If all extraverts have a wider mouth, this will indeed be present in the composite image, while irrelevant features will be blended away. However, it is possible that there is more than one way for extraverts to manifest this trait facially, e.g., one person may have a wider mouth while another has a longer nose. Perhaps both of these extraverts can be accurately identified as such, but if a composite image were made of their faces, the different signals of extraversion would be decreased. Future research might investigate this idea by comparing the accuracy of trait perceptions using both composite and individual images.

As I discussed earlier, our initial evidence of personality information in the chimpanzee face is only the first step in demonstrating a shared signalling system across species. Our next step is to replicate our findings with a new set of chimpanzees, photographs, and personality ratings. We might also attempt to address potential criticisms due to idiosyncrasies in the stimuli by averaging the ratings of several photographs, or creating prototype images of individual chimpanzees by averaging multiple photographs. Using this type of stimulus, we could minimise possible effects due to lighting, posture, and other irrelevant features particular to individual photographs. This second demonstration of signals from the chimpanzee face would strengthen our initial findings, and would allow an extension in order to investigate whether information other than dominance was signalled from the face.

Future research would also greatly benefit from considering the ‘chimpanzee side’ of the equation. By utilising chimpanzees as participants through the use of touchscreen technology, we might better understand what information is accessible to the chimpanzees from the face, complementing our previous work which only informed us about what information is present.

Conclusion

The main goals of my thesis were to make significant headway in understanding personality signals from the human face, and to identify where in the face these signals are located. Further, I aimed to investigate the hypothesis of a shared signal system that is also present in chimpanzees, and to provide the first evidence of its existence. The research contained in this thesis has succeeded in these goals by identifying information signalled from the human face, where in the face these signals are carried, and that these signals are also present in the chimpanzee face. It is the challenge of future research to demonstrate that chimpanzees are also able to receive these signals, and that the similarities in the two signal systems may mean that they can read information in the human face.

REFERENCES

- Ackermann, R. R. (2005). Ontogenetic integration of the hominoid face. *Journal of Human Evolution*, *48*, 175-197.
- Alvergne, A., Huchard, E., Caillaud, D., Charpentier, M. J. E., Setchell, J. M., & Ruppli, C., . . . Raymond, M. (2009). Human ability to recognize kin visually within primates. *International Journal of Primatology*, *30*, 199-210.
- Anestis, S. F., Bribiescas, R. G., & Hasselschwert, D. L. (2006). Age, rank, and personality effects on the cortisol sedation stress response in young chimpanzees. *Physiology and Behavior*, *89*, 287-294.
- Archer, J. (2006). Testosterone and human behavior: An evaluation of the challenge hypothesis. *Neuroscience and Biobehavioral Reviews*, *30*, 319-345.
- Bard, K. A., Gaspar, A. D., & Vick, S. J. (2011). Chimpanzee faces under the magnifying glass: Emerging methods reveal cross-species similarities and individuality. In A. Weiss, J. E. King, & L. Murray (Eds.), *Personality and temperament in nonhuman primates* (pp. 193-231). New York: Springer.
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, *31*(1), 5-17.
- Barth, J., Reaux, J. E., & Povinelli, D. J. (2005). Chimpanzees' (*Pan troglodytes*) use of gaze cues in object-choice tasks: different methods yield different results. *Animal Cognition*, *8*, 84-92.
- Bassili, J. N. (1979). Emotion recognition: The role of facial movement and the relative importance of upper and lower areas of the face. *Journal of Personality and Social Psychology*, *37*, 2049-2058.
- Bastir, M., & Rosas, A. (2004). Facial heights: Evolutionary relevance of postnatal ontogeny for facial orientation and skull morphology in humans and chimpanzees. *Journal of Human Evolution*, *47*, 359-381.
- Benson, P. L., Karabenick, S. A., & Lerner, R. M. (1976). Pretty pleases: The effects of physical attractiveness, race, and sex on receiving help. *Journal of Experimental Social Psychology*, *12*, 409-415.
- Berry, D. S., & Wero, J. L. F. (1993). Accuracy in face perception: A view from ecological psychology. *Journal of Personality*, *61*, 497-520.

- Berry, D. S., & Zebrowitz McArthur, L. (1985). Some components and consequences of a babyface. *Journal of Personality and Social Psychology, 48*, 312-323.
- Boothroyd, L. G., Cross, C. P., Gray, A. W., Coombes, C., & Gregson-Curtis, K. (2011). Perceiving the facial correlates of sociosexuality: Further evidence. *Personality and Individual Differences, 50*, 422-425.
- Boothroyd, L. G., Jones, B. C., Burt, D. M., DeBruine, L. M., & Perrett, D. I. (2008). Facial correlates of sociosexuality. *Evolution and Human Behavior, 29*, 211-218.
- Bouchard, T. J., & Loehlin, J. C. (2001). Genes, evolution, and personality. *Behavior Genetics, 31*(3), 243-273.
- Bower, S., Suomi, S. J., & Paukner, A. (2011). Evidence for kinship information contained in the rhesus macaque (*Macaca mulatta*) face. *Journal of Comparative Psychology*. Advance online publication.
- Boysen, S. T., & Berntson, G. G. (1989). Conspecific recognition in the chimpanzee: Cardiac responses to significant others. *Journal of Comparative Psychology, 103*, 215-220.
- Briton, N. J., & Hall, J. A. (1995). Beliefs about female and male nonverbal communication. *Sex Roles, 32*, 79-90.
- Budaev, S. V. (1997). "Personality" in the guppy (*Poecilia reticulata*): A correlational study of exploratory behavior and social tendency. *Journal of Comparative Psychology, 111*, 399-411.
- Buirski, P., Plutchik, R., & Kellerman, H. (1978). Sex differences, dominance, and personality in the chimpanzee. *Animal Behaviour, 26*, 123-129.
- Burrows, A. M., Waller, B. M., Parr, L. A., & Bonar, C. J. (2006). Muscles of facial expression in the chimpanzee (*Pan troglodytes*): descriptive, comparative and phylogenetic contexts. *Journal of Anatomy, 208*, 153-167.
- Burt, D. M., & Perrett, D. I. (1997). Perceptual asymmetries in judgements of facial attractiveness, age, gender, speech and expression. *Neuropsychologia, 35*, 685-693.
- Butler, S., Gilchrist, I. D., Burt, D. M., Perrett, D. I., Jones, E., & Harvey, M. (2005). Are the perceptual biases found in chimeric face processing reflected in eye-movement patterns? *Neuropsychologia, 43*, 52-59.
- Capitano, J. P. (1999). Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *American Journal of Primatology, 47*, 299-320.
- Carré, J. M., & McCormick, C. M. (2008). In your face: facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. *Proceedings of the Royal Society of London B, 275*, 2651-2656.

- Carré, J. M., McCormick, C. M., & Mondloch, C. J. (2009). Facial structure is a reliable cue of aggressive behavior. *Psychological Science, 20*, 1194-1198.
- Champoux, M., Higley, J. D., & Suomi, S. J. (1997). Behavioral and physiological characteristics of Indian and Chinese-Indian hybrid rhesus macaque infants. *Developmental Psychobiology, 31*, 49-63.
- Coetsee, V., Chen, J., Perrett, D. I., & Stephen, I. D. (2010). Deciphering faces: Quantifiable visual cues to weight. *Perception, 39*, 51-61.
- Coetsee, V., Perrett, D. I., & Stephen, I. D. (2009). Facial adiposity: A cue to health? *Perception, 38*, 1700-1711.
- Connolly, J. J., Kavanagh, E. J., & Viswesvaran, C. (2007). The convergent validity between self and observer ratings of personality: A meta-analytic review. *International Journal of Selection and Assessment, 15*, 110-117.
- Costa, P. T., Jr., & McCrae, R. R. (1980). Influence of extraversion and neuroticism on subjective well-being: Happy and unhappy people. *Journal of Personality and Social Psychology, 38*, 668-678.
- Davis, M. H. (1980). A multidimensional approach to individual differences in empathy. *JSAS Catalog of Selected Documents in Psychology, 10*(4), 85.
- Dawkins, R., & Krebs, J. R. (1978). Animal signals: Information or manipulation? In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (1st ed., pp. 282-309). Oxford: Blackwell.
- Dawson, G., Webb, S. J., & McPartland, J. (2005). Understanding the nature of face processing impairment in autism: insights from behavioral and electrophysiological studies. *Developmental Neuropsychology, 27*(3), 403-424.
- Deaner, R. O., Khera, A. V., & Platt, M. L. (2005). Monkeys pay per view: Adaptive valuation of social images by rhesus macaques. *Current Biology, 15*, 543-548.
- de Waal, F. B. M. (2000). *Chimpanzee politics: Power and sex among apes* (Rev. ed.). Baltimore: Johns Hopkins University Press.
- Dion, K. L., Berscheid, E., & Walster, E. (1972). What is beautiful is good. *Journal of Personality and Social Psychology, 24*, 285-290.
- Donnellan, M. B., Oswald, F. L., Baird, B. M., & Lucas, R. E. (2006). The Mini-IPIP scales: Tiny-yet-effective measures of the Big Five factors of personality. *Psychological Assessment, 18*, 192-203.

- Dufour, V., Pascalis, O., & Petit, O. (2006). Face processing limitation to own species in primates: A comparative study in brown capuchins, Tonkean macaques and humans. *Behavioural Processes, 73*, 107-113.
- Dutton, D. M. (2008). Subjective assessment of chimpanzee (*Pan troglodytes*) personality: reliability and stability of trait ratings. *Primates, 49*, 253-259.
- Ekman, P., & Friesen, W. (1978). *Facial action coding system: A technique for the measurement of facial movement*. Palo Alto, CA: Consulting Psychologists Press.
- Ekman, P., Friesen, W. V., O'Sullivan, M., Chan, A., Diacoyanni-Tarlatzis, I., Heider, K., . . . Tzavaras, A. (1987). Universals and cultural differences in the judgments of facial expressions of emotion. *Journal of Personality and Social Psychology, 53*, 712-717.
- Eysenck, H. (1992). Four ways five factors are not basic. *Personality and Individual Differences, 13*, 667-674.
- Eysenck, H. J., & Eysenck, M. W. (1985). *Personality and individual differences: A natural science approach*. New York: Plenum Press.
- Farkas, L. G., & Cheung, G. (1981). Facial asymmetry in healthy North American caucasians. *Angle Orthodontist, 61*, 70-77.
- Feingold, A. (1992). Good-looking people are not what we think. *Psychological Bulletin, 111*, 304-341.
- Fernández-Carriba, S., Loeches, A., Morcillo, A., & Hopkins, W. D. (2002). Functional asymmetry of emotions in primates: New findings in chimpanzees. *Brain Research Bulletin, 57*, 561-564.
- Ferrario, V. F., Sforza, C., Miani, A., Jr., & Serrao, G. (1995). A three-dimensional evaluation of human facial asymmetry. *Journal of Anatomy, 186*, 103-110.
- Fink, B., Neave, N., Manning, J. T., & Grammer, K. (2005). Facial symmetry and the 'big-five' personality factors. *Personality and Individual Differences, 39*, 523-529.
- Fink, B., & Penton-Voak, I. S. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science, 11*, 154-158.
- Fletcher-Watson, S., Findlay, J. M., Leekam, S. R., & Benson, V. (2008). Rapid detection of person information in a naturalistic scene. *Perception, 37*, 571-583.
- Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: a review and evaluation of past research. *American Journal of Primatology, 71*, 1-19.
- Funder, D. C., Kolar, D. C., & Blackman, M. C. (1995). Agreement among judges of personality: interpersonal relations, similarity, and acquaintanceship. *Journal of Personality and Social Psychology, 69*, 656-672.

- Gangestad, S. W., Thornhill, R., & Garver, C. E. (2002). Changes in women's sexual interests and their partners' mate retention tactics across the menstrual cycle: Evidence for shifting conflicts of interest. *Proceedings of the Royal Society of London B*, *269*, 975-982.
- Goldberg, L. R. (1990). An alternative "description of personality": The Big-Five factor structure. *Journal of Personality and Social Psychology*, *59*(6), 1216-1229.
- Goldberg, L. R. (1993). The structure of phenotypic personality traits. *American Psychologist*, *48*(1), 26-34.
- Gosling, S. D. (1998). Personality dimensions in spotted hyenas (*Crocuta crocuta*). *Journal of Comparative Psychology*, *112*, 107-118.
- Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*, 45-86.
- Gosling, S. D., & John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, *8*, 69-75.
- Gosling, S. D., & Vazire, S. (2002). Are we barking up the right tree? Evaluating a comparative approach to personality. *Journal of Research in Personality*, *36*, 607-614.
- Gow, A. J., Whiteman, M. C., Pattie, A., & Deary, I. J. (2005). Goldberg's 'IPIP' Big-Five factor markers: Internal consistency and concurrent validation in Scotland. *Personality and Individual Differences*, *39*, 317-329.
- Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, *144*, 517-546.
- Grammer, K., Fink, B., Møller, A. P., & Manning, J. T. (2005). Physical attractiveness and health: Comment on Weeden and Sabini (2005). *Psychological Bulletin*, *131*, 658-661.
- Grammer, K., Fink, B., Møller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: Sexual selection and the biology of beauty. *Biological Review*, *78*, 385-407.
- Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, *108*, 233-242.
- Hamermesh, D., & Biddle, J. (1994). Beauty and the labor market. *American Economic Review*, *84*, 1174-1194.
- Haselhuhn, M. P., & Wong, E. M. (2011). Bad to the bone: facial structure predicts unethical behaviour. *Proceedings of the Royal Society of London B*. Advance online publication.
- Hassin, R., & Trope, Y. (2000). Facing faces: Studies on the cognitive aspects of physiognomy. *Journal of Personality and Social Psychology*, *78*, 837-852.
- Hasson, O. (1994). Cheating signals. *Journal of Theoretical Biology*, *167*, 223-268.

- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4, 223-233.
- Hommel, B., & Lippa, Y. (1995). S-R compatibility effects due to context-dependent spatial stimulus coding. *Psychonomic Bulletin & Review*, 2, 370-374.
- Hönekopp, J. (2006). Once more: Is beauty in the eye of the beholder? Relative contributions of private and shared taste to judgments of facial attractiveness. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 199-209.
- Hönekopp, J., Bartholomé, T., & Jansen, G. (2004). Facial attractiveness, symmetry, and physical fitness in young women. *Human Nature*, 15, 147-167.
- Hong, K. W., Weiss, A., Morimura, N., Udono, T., Hayasaka, I., Humle, T., . . . Inoue-Murayama, M. (2011). Polymorphism of the Tryptophan Hydroxylase 2 (TPH2) gene is associated with chimpanzee neuroticism. *PLoS ONE*, 6, e22144.
- Hope, D., Bates, T., Penke, L., Gow, A. J., Starr, J. M., & Deary, I. J. (2011). Fluctuating asymmetry and personality. *Personality and Individual Differences*, 50, 49-52.
- Izard, C. E. (1971). *The face of emotion*. New York: Appleton-Century-Crofts.
- Jelenkovic, A., Poveda, A., Susanne, C., & Rebato, E. (2010). Common genetic and environmental factors among craniofacial traits in Belgian nuclear families: Comparing skeletal and soft-tissue related phenotypes. *HOMO - Journal of Comparative Human Biology*, 61, 191-203.
- John, O. P. & Srivastava, S. (1999). The Big-Five Trait Taxonomy: History, Measurement, and Theoretical Perspectives. In L. A. Pervin & O. P. John (Eds.), *Handbook of personality: Theory and research* (2nd ed.) (pp. 102-139). New York: Guilford Press.
- Johnson, B. R. (2010). Task partitioning in honey bees: the roles of signals and cues in group-level coordination of action. *Behavioral Ecology*, 21, 1373-1379.
- Johnston, V. S., & Franklin, M. (1993). Is beauty in the eye of the beholder? *Ethology and Sociobiology*, 14, 183-199.
- Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: evidence for a hormone-mediated adaptive design. *Evolution and Human Behavior*, 22, 251-267.
- Jones, B. C., DeBruine, L. M., Main, J. C., Little, A. C., Welling, L. L. M., Feinberg, D. R., & Tiddeman, B. P. (2010). Facial cues of dominance modulate the short-term gaze-cuing effect in human observers. *Proceedings of the Royal Society of London B*, 277, 617-624.

- Jones, A., Kramer, R. S. S., & Ward, R. (in press). Signals of personality and health: The contributions of facial shape, skin texture and viewing angle. *Journal of Experimental Psychology: Human Perception and Performance*.
- Kalick, S. M., Zebrowitz, L. A., Langlois, J. H., & Johnson, R. M. (1998). Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychological Science, 9*, 8-13.
- Kano, F., & Tomonaga, M. (2010). Face scanning in chimpanzees and humans: continuity and discontinuity. *Animal Behaviour, 79*, 227-235.
- King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality, 31*, 257-271.
- King, J. E., & Landau, V. I. (2003). Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *Journal of Research in Personality, 37*, 1-15.
- King, J. E., Weiss, A., & Sisco, M. M. (2008). Aping humans: Age and sex effects in chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) personality. *Journal of Comparative Psychology, 122*, 418-427.
- Knutson, B. (1996). Facial expressions of emotion influence interpersonal trait inferences. *Journal of Nonverbal Behavior, 20*, 165-182.
- Koba, R., Izumi, A., & Nakamura, K. (2009). Sexual dimorphism in facial shapes and their discrimination in Japanese monkeys (*Macaca fuscata*). *Journal of Comparative Psychology, 123*, 326-333.
- Kowner, R. (1995). Laterality in facial expressions and its effect on attributions of emotion and personality: A reconsideration. *Neuropsychologia, 33*, 539-559.
- Kramer, R. S. S., Arend, I., & Ward, R. (2010). Perceived health from biological motion predicts voting behaviour. *The Quarterly Journal of Experimental Psychology, 63*, 625-632.
- Kramer, R. S. S., King, J., & Ward, R. (2011). Identifying personality from the static, nonexpressive face in humans and chimpanzees: evidence of a shared system for signaling personality. *Evolution and Human Behavior, 32*, 179-185.
- Kramer, R. S. S., & Ward, R. (2010). Internal facial features are signals of personality and health. *The Quarterly Journal of Experimental Psychology, 63*, 2273-2287.
- Kramer, R. S. S., & Ward, R. (2011). Different signals of personality and health from the two sides of the face. *Perception, 40*, 549-562.

- Krebs, J. R., & Dawkins, R. (1984). Animal signals: Mind-reading and manipulation. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (2nd ed., pp. 380-402). Oxford: Blackwell.
- Kumar, S., Filipowski, A., Swarna, V., Walker, A., & Blair Hedges, S. (2005). Placing confidence limits on the molecular age of the human-chimpanzee divergence. *Proceedings of the National Academy of Sciences*, *102*, 18842-18847.
- Law Smith, M. J., Perrett, D. I., Jones, B. C., Cornwell, R. E., Moore, F. R., Feinberg, D. R., . . . Hillier, S. G. (2006). Facial appearance is a cue to oestrogen levels in women. *Proceedings of the Royal Society of London B*, *273*, 135-140.
- Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2003). Expert face processing requires visual input to the right hemisphere during infancy. *Nature Neuroscience*, *6*, 1108-1112.
- Li, J., Tian, M., Fang, H., Xu, M., Li, H., & Liu, J. (2010). Extraversion predicts individual differences in face recognition. *Communicative & Integrative Biology*, *3*, 295-298.
- Lieberman, D. E. (2011). *The evolution of the human head*. Cambridge, MA: Belknap Press of Harvard University Press.
- Lilienfeld, S. O., Gershon, J., Duke, M., Marino, L., & de Waal, F. B. M. (1999). A preliminary investigation of the construct of psychopathic personality (psychopathy) in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *113*, 365-375.
- Lindell, A. K., & Savill, N. J. (2010). Time to turn the other cheek? The influence of left and right poses on perceptions of academic specialisation. *Laterality*, *15*, 639-650.
- Little, A. C., Burt, D. M., & Perrett, D. I. (2006). What is good is beautiful: Face preference reflects desired personality. *Personality and Individual Differences*, *41*, 1107-1118.
- Little, A. C., & Hancock, P. J. B. (2002). The role of masculinity and distinctiveness in judgments of human male facial attractiveness. *British Journal of Psychology*, *93*, 451-464.
- Little, A. C., McPherson, J., Dennington, L., & Jones, B. C. (2011). Accuracy in assessment of self-reported stress and a measure of health from static facial information. *Personality and Individual Differences*, *51*, 693-698.
- Little, A. C., & Perrett, D. I. (2007). Using composite images to assess accuracy in personality attribution to faces. *British Journal of Psychology*, *98*, 111-126.
- Malatesta, C. Z., Fiore, M. J., & Messina, J. J. (1987). Affect, personality, and facial expressive characteristics of older people. *Psychology and Aging*, *2*, 64-69.

- Maninger, N., Capitanio, J. P., Mendoza, S. P., & Mason, W. A. (2003). Personality influences tetanus-specific antibody response in adult male rhesus macaques after removal from natal group and housing relocation. *American Journal of Primatology*, *61*, 73-83.
- Marlowe, C. M., Schneider, S. L., & Nelson, C. E. (1996). Gender and attractiveness biases in hiring decisions: Are more experienced managers less biased? *Journal of Applied Psychology*, *81*, 11-21.
- Martin-Malivel, J., & Okada, K. (2007). Human and chimpanzee face recognition in chimpanzees (*Pan troglodytes*): Role of exposure and impact on categorical perception. *Behavioral Neuroscience*, *121*, 1145-1155.
- Marty, J. M., Higham, J. P., Gadsby, E. L., & Ross, C. (2009). Dominance, coloration and social and sexual behavior in male drills (*Mandrillus leucophaeus*). *International Journal of Primatology*, *30*, 807-823.
- Mather, J. A., & Anderson, R. C. (1993). Personalities of octopuses (*Octopus rubescens*). *Journal of Comparative Psychology*, *107*, 336-340.
- Maynard-Smith, J., & Harper, D. (2003). *Animal signals*. Oxford: Oxford University Press.
- Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioral and Brain Sciences*, *21*, 353-397.
- McGuire, M. T., Raleigh, M. J., & Pollack, D. B. (1994). Personality features in Vervet monkeys: The effects of sex, age, social status, and group composition. *American Journal of Primatology*, *33*, 1-13.
- Mehta, P. H., & Gosling, S. D. (2008). Bridging human and animal research: A comparative approach to studies of personality and health. *Brain, Behavior, and Immunity*, *22*, 651-661.
- Mondloch, C. J., Lewis, T. L., Budreau, D. R., Maurer, D., Dannemiller, J. L., Stephens, B. R., & Kleiner-Gathercoal, K. A. (1999). Face perception during early infancy. *Psychological Science*, *10*, 419-422.
- Montepare, J. M., & Zebrowitz, L. A. (1998). Person perception comes of age: The salience and significance of age in social judgments. In M. P. Zanna (Ed.), *Advances in experimental social psychology* (Vol. 30, pp. 93-163). New York: Academic Press.
- Mueller, U., & Mazur, A. (1997). Facial dominance in *Homo sapiens* as honest signaling of male quality. *Behavioral Ecology*, *8*, 569-579.
- Murray, L. (2011). Predicting primate behavior from personality ratings. In A. Weiss, J. E. King, & L. Murray (Eds.), *Personality and temperament in nonhuman primates* (pp. 129-167). New York: Springer.

- Neave, N., & Shields, K. (2008). The effects of facial hair manipulation on female perceptions of attractiveness, masculinity, and dominance in male faces. *Personality and Individual Differences, 45*, 373-377.
- Nettle, D. (2006). The evolution of personality variation in humans and other animals. *American Psychologist, 61*, 622-631.
- Nicholls, M. E. R., Clode, D., Wood, S. J., & Wood, A. G. (1999). Laterality of expression in portraiture: Putting your best cheek forward. *Proceedings of the Royal Society of London B, 266*, 1517-1522.
- Nicholls, M. E. R., Wolfgang, B. J., Clode, D., & Lindell, A. K. (2002). The effect of left and right poses on the expression of facial emotion. *Neuropsychologia, 40*, 1662-1665.
- Noor, F., & Evans, D. C. (2003). The effect of facial symmetry on perceptions of personality and attractiveness. *Journal of Research in Personality, 37*, 339-347.
- Norman, W. T. (1963). Toward an adequate taxonomy of personality attributes: Replicated factor structure in peer nomination personality ratings. *Journal of Abnormal and Social Psychology, 66*, 574-583.
- Park, J. H., Buunk, A. P., & Wieling, M. B. (2007). Does the face reveal athletic flair? Positions in team sports and facial attractiveness. *Personality and Individual Differences, 43*, 1960-1965.
- Parr, L. A. (2003). The discrimination of faces and their emotional content by chimpanzees (*Pan troglodytes*). *Annals of the New York Academy of Sciences, 1000*, 56-78.
- Parr, L. A., & de Waal, F. B. M. (1999). Visual kin recognition in chimpanzees. *Nature, 399*, 647-648.
- Parr, L. A., Dove, T., & Hopkins, W. D. (1998). Why faces may be special: Evidence of the inversion effect in chimpanzees. *Journal of Cognitive Neuroscience, 10*, 615-622.
- Parr, L. A., Hecht, E., Barks, S. K., Preuss, T. M., & Votaw, J. R. (2009). Face processing in the chimpanzee brain. *Current Biology, 19*, 50-53.
- Parr, L. A., Heintz, M., & Akamagwuna, U. (2006). Three studies on 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: (*Pan troglodytes* and *Macaca mulatta*): Inbreeding avoidance or male distinctiveness? *Journal of Comparative Psychology, 124*, 343-350.
- Parr, L. A., Waller, B. M., Vick, S. J., & Bard, K. A. (2007). Classifying chimpanzee facial expressions using muscle action. *Emotion, 7*(1), 172-181.

- 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.
- Paunonen, S. V. (2003). Big Five factors of personality and replicated predictions of behavior. *Journal of Personality and Social Psychology*, *84*, 411-422.
- Paunonen, S. V., & Ashton, M. C. (2001). Big Five factors and facets and the prediction of behavior. *Journal of Personality and Social Psychology*, *81*, 524-539.
- Pederson, A. K., King, J. E., & Landau, V. I. (2005). Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality*, *39*, 534-549.
- Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior*, *25*, 229-241.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., & Minamisawa, R. (1999). Menstrual cycle alters face preference. *Nature*, *394*, 884-887.
- Penton-Voak, I. S., Pound, N., Little, A. C., & Perrett, D. I. (2006). Personality judgments from natural and composite facial images: More evidence for a “kernel of truth” in social perception. *Social Cognition*, *24*, 490-524.
- Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., . . . Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, *394*, 884-887.
- Pokorny, J. J., & de Waal, F. B. M. (2009). Monkeys recognize the faces of group mates in photographs. *Proceedings of the National Academy of Sciences*, *106*, 21539-21543.
- Polak, M. (Ed.). (2003). *Developmental instability: Causes and consequences*. Oxford: Oxford University Press.
- Pound, N., Penton-Voak, I. S., & Brown, W. M. (2007). Facial symmetry is positively associated with self-reported extraversion. *Personality and Individual Differences*, *43*, 1572-1582.
- Reis, V. A., & Zaidel, D. W. (2001). Functional asymmetry in the human face: Perception of health in the left and right sides of the face. *Laterality*, *6*, 225-231.
- Reynolds, S. K., & Clark, L. A. (2001). Predicting dimensions of personality disorder from domains and facets of the five-factor model. *Journal of Personality*, *69*, 199-222.
- Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? *Proceedings of the Royal Society of London B (Suppl.)*, *270*, S93-95.

- Rhodes, G., Louw, K., & Evangelista, E. (2009). Perceptual adaptation to facial asymmetries. *Psychonomic Bulletin & Review*, *16*, 503-508.
- Rhodes, G., Proffitt, F., Grady, J., & Sumich, A. (1998). Facial symmetry and the perception of beauty. *Psychonomic Bulletin and Review*, *5*, 659-669.
- Rhodes, G., Yoshikawa, S., Palermo, R., Simmons, L. W., Peters, M., Lee, K., . . . Crawford, J. R. (2007). Perceived health contributes to the attractiveness of facial symmetry, averageness, and sexual dimorphism. *Perception*, *36*, 1244-1252.
- Rhodes, G., Zebrowitz, L. A., Clark, A., Kalick, S. M., Hightower, A., & McKay, R. (2001). Do facial averageness and symmetry signal health? *Evolution and Human Behavior*, *22*, 31-46.
- Riemann, R., Angleitner, A., & Strelau, J. (1997). Genetic and environmental influences on personality: A study of twins reared together using the self- and peer report NEO-FFI scales. *Journal of Personality*, *65*, 449-475.
- Roether, C. L., Omlor, L., & Giese, M. A. (2008). Lateral asymmetry of bodily emotion expression. *Current Biology*, *18*, R329-R330.
- Rojas, Q. M., Masip, D., Todorov, A., & Vitria, J. (2011). Automatic prediction of facial trait judgments: Appearance vs structural models. *PLoS ONE*, *6*, e23323.
- Rosenthal, R., Hall, J. A., DiMatteo, M. R., Rogers, P. L., & Archer, D. (1979). *Sensitivity to nonverbal communication: The PONS test*. Baltimore: The Johns Hopkins University Press.
- Rowland, D. A., & Perrett, D. I. (1995). Manipulating facial appearance through shape and color. *IEEE Computer Graphics and Applications*, *15*, 70-76.
- Rule, N. O., & Ambady, N. (2010). Democrats and Republicans can be differentiated by their faces. *PLoS ONE*, *5*, e8733.
- Rule, N. O., Ambady, N., Adams, R. B., Jr., & Macrae, C. N. (2008). Accuracy and awareness in the perception and categorization of male sexual orientation. *Journal of Personality and Social Psychology*, *95*, 1019-1028.
- Rule, N. O., Ambady, N., & Hallett, K. C. (2009). Female sexual orientation is perceived accurately, rapidly, and automatically from the face and its features. *Journal of Experimental Social Psychology*, *45*, 1245-1251.
- Rule, N. O., Garrett, J. V., & Ambady, N. (2010). On the perception of religious group membership from faces. *PLoS ONE*, *5*, e14241.
- Sackeim, H. A., Gur, R. C., & Saucy, M. C. (1978). Emotions are expressed more intensely on the left side of the face. *Science*, *202*, 434-436.

- Sapolsky, R. M. (1999). Hormonal correlates of personality and social contexts: from non-human to human primates. In C. Panter-Brick & C. M. Worthman (Eds.), *Hormones, health, and behavior: A socio-ecological and lifespan perspective* (pp. 18-46). New York: Cambridge University Press.
- Saulsman, L. M., & Page, A. C. (2004). The five-factor model and personality disorder empirical literature: A meta-analytic review. *Clinical Psychology Review, 23*, 1055-1085.
- Saxton, T. K., Burriss, R. P., Murray, A. K., Rowland, H. M., & Roberts, S. G. (2009). Face, body and speech cues independently predict judgments of attractiveness. *Journal of Evolutionary Psychology, 7*, 23-35.
- Setchell, J. M., & Wickings, E. J. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology, 111*, 25-50.
- Shackelford, T. K., & Larsen, R. J. (1999). Facial attractiveness and physical health. *Evolution and Human Behavior, 20*, 71-76.
- Shepherd, S. V., Deaner, R. O., & Platt, M. L. (2006). Social status gates attention in monkeys. *Current Biology, 16*, R119-120.
- Shevlin, M., Walker, S., Davies, M. N. O., Banyard, P., & Lewis, C. A. (2003). Can you judge a book by its cover? Evidence of self-stranger agreement on personality at zero acquaintance. *Personality and Individual Differences, 35*, 1373-1383.
- Simmons, L. W., Rhodes, G., Peters, M., & Koehler, N. (2004). Are human preferences for facial symmetry focused on signals of developmental instability? *Behavioral Ecology, 15*, 864-871.
- Sitton, S. C., Waite, L., & Rivers, S. C. (2006). Perception of traits from normal, mirror and chimeric images of faces. *American Journal of Psychological Research, 2*, 14-20.
- Stephen, I. D., Coetzee, V., Law Smith, M., & Perrett, D. I. (2009). Skin blood perfusion and oxygenation colour affect perceived human health. *PLoS ONE, 4*, e5083.
- Sternglanz, S. H., Gray, J. L., & Murakami, M. (1977). Adult preferences for infantile facial features: An ethological approach. *Animal Behavior, 25*, 108-115.
- Stevenson-Hinde, J., Stillwell-Barnes, R., & Zunz, M. (1980). Subjective assessment of rhesus monkeys over four successive years. *Primates, 21*, 66-82.
- Stillman, T. F., Maner, J. K., & Baumeister, R. F. (2010). A thin slice of violence: distinguishing violent from nonviolent sex offenders at a glance. *Evolution and Human Behavior, 31*, 298-303.
- Stirrat, M., & Perrett, D. I. (2010). Valid facial cues to cooperation and trust: male facial width and trustworthiness. *Psychological Science, 21*, 349-354.

- Strand Viðarsdóttir, U., O'Higgins, P., & Stringer, C. (2002). A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton. *Journal of Anatomy*, 201, 211-229.
- Swaddle, J. P., & Reiersen, G. W. (2002). Testosterone increases perceived dominance but not attractiveness of human males. *Proceedings of the Royal Society of London B*, 269, 2285-2289.
- Tamura, S., Kawai, H., & Mitsumoto, H. (1996). Male/female identification from 8 x 6 very low resolution face images by neural network. *Pattern Recognition*, 29, 331-335.
- Tanner, J. M. (1978). *Foetus into man: Physical growth from conception to maturity*. London: Open Books.
- Taubert, J. (2009). Chimpanzee faces are 'special' to humans. *Perception*, 38, 343-356.
- ten Cate, C. (2002). Posing as professor: Laterality in posing orientation for portraits of scientists. *Journal of Nonverbal Behavior*, 26, 175-192.
- Tett, R. P., Jackson, D. N., & Rothstein, M. (1991). Personality measures as predictors of job performance: A meta-analytic review. *Personnel Psychology*, 44, 703-742.
- Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, 3, 452-460.
- Thornhill, R., & Møller, A. P. (1997). Developmental stability, disease and medicine. *Biological Reviews*, 72, 497-548.
- Tomonaga, M. (2007). Is chimpanzee (*Pan troglodytes*) spatial attention reflexively triggered by the gaze cue? *Journal of Comparative Psychology*, 121, 156-170.
- Tupes, E. C., & Christal, R. E. (1992). Recurrent personality factors based on trait ratings. *Journal of Personality*, 60, 225-251.
- Uher, J., & Asendorpf, J. B. (2008). Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality*, 42, 821-838.
- Valla, J. M., Ceci, S. J., & Williams, W. M. (2011). The accuracy of inferences about criminality based on facial appearance. *Journal of Social, Evolutionary, and Cultural Psychology*, 5, 66-91.
- Van Valen, L. (1962). A study of fluctuating asymmetry. *Evolution*, 16, 125-142.
- Vazire, S., Gosling, S. D., Dickey, A. S., & Schapiro, S. J. (2007). Measuring personality in nonhuman animals. In R. W. Robins, R. C. Fraley, & R. F. Krueger (Eds.), *Handbook of research methods in personality psychology* (pp. 190-206). New York: Guilford.

- Verdonck, A., Gaethofs, M., Carels, C., & de Zegher, F. (1999). Effect of low-dose testosterone treatment on craniofacial growth in boys with delayed puberty. *European Journal of Orthodontics*, *21*, 137-143.
- Vick, S. J., Waller, B. M., Parr, L. A., Smith Pasqualini, M. C., & Bard, K. A. (2007). A cross-species comparison of facial morphology and movement in humans and chimpanzees using the facial action coding system (FACS). *Journal of Nonverbal Behavior*, *31*, 1-20.
- Vokey, J. R., Rendall, D., Tangen, J. M., Parr, L. A., & de Waal, F. B. M. (2004). Visual kin recognition and family resemblance in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *118*, 194-199.
- Ware, J. E., Jr., Kosinski, M., & Keller, S. D. (1996). A 12 item short form health survey: Construction of scales and preliminary tests of reliability and validity. *Medical Care*, *34*, 220-233.
- Weeden, J., & Sabini, J. (2005). Physical attractiveness and health in Western societies: A review. *Psychological Bulletin*, *131*, 635-653.
- Weiss, A., King, J. E., & Enns, R. M. (2002). Subjective well-being is heritable and genetically correlated with dominance in chimpanzees (*Pan troglodytes*). *Journal of Personality and Social Psychology*, *83*, 1141-1149.
- Weiss, A., King, J. E., & Figueredo, A. J. (2000). The heritability of personality factors in chimpanzees (*Pan troglodytes*). *Behavior Genetics*, *30*, 213-221.
- Weston, E. M., Friday, A. E., & Liò, P. (2007). Biometric evidence that sexual selection has shaped the hominin face. *PLoS ONE*, *2*, e710.
- Willis, J., & Todorov, A. (2006). First impressions: Making up your mind after a 100-ms exposure to a face. *Psychological Science*, *17*, 592-598.
- Wilson, C. E., Brock, J., & Palermo, R. (2010). Attention to social stimuli and facial identity recognition skills in autism spectrum disorder. *Journal of Intellectual Disability Research*, *54*, 1104-1115.
- Wyatt, T. D. (2010). Pheromones and signature mixtures: defining species-wide signals and variable cues for identity in both invertebrates and vertebrates. *Journal of Comparative Physiology A*, *196*, 685-700.
- Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology*, *53*, 205-214.

- Zaidel, D. W., Chen, A. C., & German, C. (1995). She is not a beauty even when she smiles: Possible evolutionary basis for a relationship between facial attractiveness and hemispheric specialization. *Neuropsychologia*, *33*, 649-655.
- Zajonc, R. B., Adelman, P. K., Murphy, S. T., & Niedenthal, P. M. (1987). Convergence in the physical appearance of spouses. *Motivation and Emotion*, *11*, 335-346.
- Zebrowitz, L. A. (1999). *Reading faces: Window to the soul?* Boulder, CO: Westview.
- Zebrowitz, L. A., & Collins, M. A. (1997). Accurate social perception at zero acquaintance: The affordances of a Gibsonian approach. *Personality and Social Psychology Review*, *1*, 204-223.
- Zebrowitz, L. A., & Montepare, J. M. (2008). First impressions from facial appearance cues. In N. Ambady & J. J. Skowronski (Eds.), *First impressions* (pp. 171-204). New York: Guilford.
- Zebrowitz, L. A., & Rhodes, G. (2004). Sensitivity to “bad genes” and the anomalous face overgeneralization effect: Cue validity, cue utilization, and accuracy in judging intelligence and health. *Journal of Nonverbal Behavior*, *28*, 167-185.

APPENDIX

Table 1: Accuracy on forced-choice (two alternative) discrimination for the Big 5 personality traits, and for Health, as measured by the PCS sub-scale of the SF-12. Values are percentages, and chance performance is 50%. Accuracy is illustrated for Trait, Face Side, and Face Type.

Trait	Face Side	Face Type	Mean	Std. Error	95% Confidence Interval	
					Lower Bound	Upper Bound
Agreeableness	Left	Original	53.1	3.8	45.4	60.9
		Mirrored	57.8	4	49.7	66
	Right	Original	62.9	3.3	56.2	69.6
		Mirrored	53.9	3.7	46.4	61.4
Conscientiousness	Left	Original	43	3.1	36.7	49.2
		Mirrored	42.6	3.7	35.1	50.1
	Right	Original	47.3	3	41.2	53.3
		Mirrored	43	4.2	34.5	51.5
Extraversion	Left	Original	72.3	3.6	65	79.6
		Mirrored	72.7	3.5	65.5	79.8
	Right	Original	60.5	3.6	53.3	67.8
		Mirrored	64.5	3.6	57	71.9
Intellect/Imagination	Left	Original	44.9	2.9	39	50.9
		Mirrored	47.7	2.7	42.2	53.1
	Right	Original	55.9	2.6	50.5	61.2
		Mirrored	47.7	3.1	41.3	54
Emotional Stability	Left	Original	62.5	3.8	54.7	70.3
		Mirrored	57	4.1	48.6	65.4
	Right	Original	70.7	3.5	63.6	77.8
		Mirrored	60.9	4.1	52.6	69.3
Health	Left	Original	54.3	3.1	48.1	60.5
		Mirrored	53.1	4.3	44.3	61.9
	Right	Original	67.6	3.7	60.1	75.1
		Mirrored	66.4	4.3	57.6	75.2