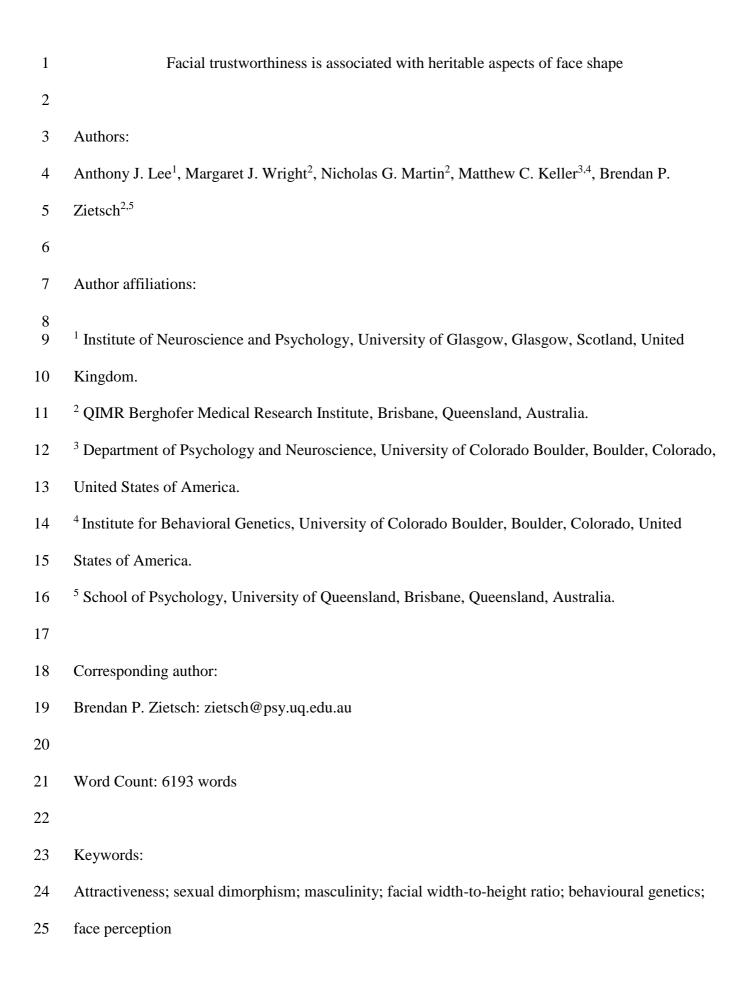
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27 Abstract

Facial trustworthiness is thought to underlie social judgements in face perception, though it is unclear whether trustworthiness judgements are based on stable facial attributes. If this were the case, we could expect a genetic component of facial trustworthiness. From facial photographs of a large sample of identical and nonidentical twins and siblings (1320 individuals), we tested for genetic variation in facial trustworthiness and genetic covariation with several stable facial attributes, including facial attractiveness, two measures of masculinity, and facial width-to-height ratio. We found a significant genetic component of facial trustworthiness in men (but not women), and significant genetic correlations with the stable morphological facial traits of attractiveness, perceived masculinity, and facial width-to-height ratio. However, there was no significant genetic or shared environmental correlation between facial trustworthiness and an objective masculinity score based on facial landmark coordinates, despite there being a significant phenotypic correlation. Our results suggest that heritable facial traits influence trustworthiness judgements.

Facial trustworthiness has been proposed to be one of the key dimensions that underlie social judgements in face perception (Oosterhof & Todorov, 2008). Indeed, facial trustworthiness judgements has been found to predict outcomes in reality; for instance, convicted murderers with trustworthy faces are less likely to receive the death sentence compared to those with untrustworthy faces (J. P. Wilson & Rule, 2015). In elections, results can be predicted based on the facial trustworthiness of the candidates (Little, Roberts, Jones, & DeBruine, 2012; Mattes et al., 2010). Facial trustworthiness also appears to influence online purchasing decisions, with individuals more likely to choose a vendor with a trustworthy face regardless of the presence of more objective trustworthy indicators such as reviews (Ert, Fleischer, & Magen, 2016). In more controlled settings, participants are more likely to invest in a partner high in facial trustworthiness in various economic games (van 't Wout & Sanfey, 2008).

Trustworthiness is thought to underlie social judgements because it conveys pivotal social information (Oosterhof & Todorov, 2008). Accurately assessing the trustworthiness of others is important because trusting an untrustworthy individual could have severe negative consequences, while not trusting a trustworthy individual results in a missed opportunity for cooperation (Cosmides & Tooby, 1992). Such judgements are useful before engaging with an individual, and are dynamically updated with further experience (Chang, Doll, van 't Wout, Frank, & Sanfey, 2010). Given the importance of trustworthiness judgements, previous research has proposed that we have evolved a mechanism to evaluate trustworthiness quickly (Oosterhof & Todorov, 2008). Indeed, trustworthy judgements made on faces occur with minimal exposure (less than a second; Todorov, Pakrashi, & Oosterhof, 2009; Willis & Todorov, 2006), has high consensus between individuals (Zebrowitz, Voinescu, & Collins, 1996) and influences behaviour from a young age (Ewing, Caulfield, Read, & Rhodes, 2015).

To some degree, trustworthiness judgements are based on dynamic cues, such as emotional expression (i.e., faces expressing happiness is positively associated with trustworthiness, while those expressing anger or sadness are negatively associated; Oosterhof & Todorov, 2009; Verplaetse, Vanneste, & Braeckman, 2007). Indeed, dynamic cues such as authentic smiling (and to a lesser degree, fake smiling) have been associated with trustworthiness judgements (Krumhuber et al., 2007; Oosterhof & Todorov, 2009). Also consistent with this notion, Dotsch and Todorov (2012) identified that highly dynamic areas such as the mouth, eyes, and hair regions are particularly important when making trustworthiness judgements.

More controversial is whether trustworthiness judgements are based on stable face traits. Some researchers suggest that dynamic cues are more important for trustworthiness judgements (Hehman, Flake, & Freeman, 2015), while other suggests that 'unfakeable', stable traits are more important (Rezlescu, Duchaine, Olivola, & Chater, 2012). Indeed, some studies have found that trustworthiness is associated with face shape from participants adopting a neutral expression (Kleisner, Priplatova, Frost, & Flegr, 2013). One possibility is that judgements of trustworthiness based on stable traits are over-generalisation of subtle cues to emotional states (Todorov, 2008); however, trustworthiness judgements show unique brain activity independent of judgements of emotional expression (Winston, Strange, O'Doherty, & Dolan, 2002).

Two stable traits that have received attention and are thought to be associated with facial trustworthiness are facial attractiveness and facial masculinity. Attractive faces are perceived as more trustworthy (R. K. Wilson & Eckel, 2006). This could be because we may have evolved to find cues to trustworthiness attractive because trustworthy individuals are evolutionarily beneficial as a mating partner (Gangestad & Simpson, 2000; Little, Cohen, Jones, & Belsky, 2007). However, the available evidence suggests that attractive people are actually less trustworthy (Muñoz-Reyes, Pita, Arjona, Sanchez-Pages, & Turiegano, 2014; Shinada & Tamagishi, 2014; Takahashi, Tamagishi, Tanida, Kiyonari, & Kanazawa, 2006; Zaatari & Trivers, 2007). Alternatively, the association between facial attractiveness and trustworthiness could reflect a halo effect, where

attractive individuals are judged higher on positive traits in general (Eagly, Ashmore, Makhijani, & Longo, 1991; Maestripieri, Henry, & Nickels, 2017; Surawski & Ossoff, 2006; Verhulst, Lodge, & Lavine, 2010). Research on whether attractiveness is associated with perceptions of trustworthiness finds a positive relationship for women (Langlois et al., 2000; Zaidel, Bava, & Reis, 2003), and mixed results for men, with some studies finding a positive relationship (Langlois et al., 2000), and others finding no relationship (Zaidel et al., 2003).

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Facial masculinity is thought to be associated with physical dominance in men. In turn, it may be advantageous for these facially masculine men who are physically dominant to also possess untrustworthy traits (Haselhuhn & Wong, 2011), as this would give them an advantage in contexts such as resource acquisition and intrasexual competition (Little et al., 2007; Puts, 2010). Attempts to investigate this association between actual trustworthiness and facial masculinity have focused mostly on facial width-to-height ratio (fWHR), which is often considered to be a sexually dimorphic trait (Weston, Friday, & Lio, 2007), even though the best evidence suggests negligible sex differences (Kramer, 2017; Kramer, Jones, & Ward, 2012; Lefevre et al., 2012; Özener, 2012). Men with wider faces are more likely to exploit trustworthy partners in an economic game (Stirrat & Perrett, 2010), and are more willing to deceive and cheat for their own financial gain (Haselhuhn & Wong, 2011). Assuming that actual untrustworthiness is associated with masculinity more generally, this appears to follow through to trustworthiness judgements, which are negatively associated with perceived masculinity judgements (Oosterhof & Todorov, 2008), and women are less likely to find a masculine man attractive under conditions where pro-social traits are advantageous in a romantic partner (Little et al., 2007). While much research has been done with men's faces, relatively little has been done investigating the association between masculinity and trustworthiness judgements in women's faces. Also, it is unknown how trustworthiness judgements are associated with objective facial masculinity, as opposed to perceived masculinity or fWHR, the latter of which may be perceived as sexually dimorphic but objectively is not.

Here, we aim to further investigate the link between stable facial traits and facial trustworthiness. In a sample of identical and nonidentical twins who had their photos rated and analysed, we test for genetic variation in facial trustworthiness and genetic covariation with facial attractiveness, fWHR, and an objective measure of facial masculinity based on facial landmark coordinates.

125 Methods

Participants

Participants were 1320 twins and their siblings from 738 families that either took part in the Brisbane Adolescent Twin Study (BATS; Wright & Martin, 2004) or the Longitudinal Twin Study in Boulder Colorado (LTS; Rhea, Gross, Haberstick, & Corley, 2013). Twins from the BATS (N = 990) had their photographs taken as close as possible to their 16th birthday (M = 16.03 years, SD = .43 years) while their siblings (N = 121) had photographs taken close to their 18^{th} birthday (M = 17.40 years, SD = 1.19 years). Twins from the LTS (N = 209) were older than those from the BATS (M = 21.96 years, SD = .95 years).

Photographs

For twins who were part of the BATS, photographs were taken between the years 1996 and 2010. For the earliest waves of data collection, photographs were taken using film cameras and then later scanned into a digital format. For later waves, photographs were taken using digital cameras. For twins from the LTS, photographs were taken between 2001-2010. Participants from the LTS were asked to adopt a neutral facial expression, while no instructions were given to participants from the BATS. All photographs were taken under standard indoor lighting conditions.

Facial Trait Ratings. These photographs were rated on a number of traits, including facial trustworthiness, facial attractiveness, and facial masculinity (for more detail on the rating process,

see Mitchem et al., 2015). Seven research assistants rated each photograph on a 7-point scale (1 = low in a trait, 7 = high in a trait). Between-rater consistency statistics for each trait are reported in Table 1, including Cronbach's alpha and the intra-class correlation (i.e., the proportion of total variance in ratings that is between-faces compared to within).

Table 1. Between-rater consistency statistics for each rated facial attribute.

Photo Rating	Cronbach's Alpha [95% CI]	Intra-Class Correlation
Facial Trustworthiness	.56 [.53, .56]	.14
Facial Attractiveness	.87 [.86, .88]	.44
Facial Masculinity	.67 [.65, .70]	.20

Facial Width-to-Height Ratio. Two research assistants identified 31 facial landmarks for each photograph after training. For each landmark, the mean pixel coordinates of the two research assistants were used as the coordinates for that landmark. A Generalised Procrustes Analysis (GPA) was conducted using these landmark coordinates, which standardises the landmark configurations by removing non-shape information (i.e., translation, rotation, and scale effects). From these Procrustes coordinates, facial width-to-height ratio was calculated as the width of the face (between the outer edges of the most prominent part of the cheekbones) divided by the height of the face (between the centre of the hairline to the centre of the chin; see Figure 1.).

Objective Facial Masculinity Score. A data-driven facial masculinity score was calculated for each participant using geometric morphometrics, which is the statistical analysis of shape. Similar to Lee et al. (2014), we did not include landmarks around the mouth to limit the influence of facial expression on the masculinity score. The Procrustes coordinates from the GPA were transformed into shape variables via principal components analysis, which are a decomposition of the Procrustes coordinates that completely maintains the shape information and can be used in conventional statistical techniques. To compute an objective score for facial masculinity, these

shape variables were entered into a discriminant-function-analysis (DFA) with sex as the grouping variable (0 = Female, 1 = Male). The DFA produces a discriminant function that is the linear combination of the shape variables that best discriminates between male and female landmark configurations. Effectively, the discriminant function represents the sexual dimorphism dimension. As such, where individual participants score on this function represent their objective facial masculinity. The point-biserial correlation between the discriminant function score and participant sex was .67, and the correct classification rate was .82, which is in line with previous research that has used related methods to compute objective masculinity scores (Gangestad, Thornhill, & Garver-Apgar, 2010; Scott, Pound, Stephen, Clark, & Penton-Voak, 2010). For more information on the objective facial masculinity score, see Lee et al. (2014).

height

Figure 1. Dimensions used to calculate facial width-to-height ratio.

Statistical Analysis

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Identical twins share all their genes, while nonidentical twins only share on average 50% of their segregating genes, and all twins completely share family environment. Therefore, through structural equation modelling we can partition the variance of any given trait into three sources: additive genetic sources (A), shared environmental sources (C) such as familial upbringing, and residual sources (E), which includes unique environmental factors and measurement error. As is standard for twin-family designs, we conducted maximum-likelihood modelling, which determines the combination of A, C, and E that best matches the observed means, variances, and twin-pair or sibling correlations in the data (for more information, see Neale & Cardon, 1992; Posthuma et al., 2003). Differences among the means and correlations of different zygosity groups were tested by equating the relevant parameters in the model and testing the change in model fit against the change in the degrees of freedom (which is distributed as χ^2). To test whether there is a genetic association between facial trustworthiness and the stable facial traits, we used a common factors bivariate model, which estimates the correlations between the A, C, and E components between two traits (Loehlin, 1996; Neale & Cardon, 1992). Similar to the partitioning of variance in the univariate model (described above), we can use the cross-twin cross-trait correlation (in this instance, the perceived facial trustworthiness of one twin and the other stable facial trait of the other twin) to partition the covariance between traits into genetic correlation (rA), common environmental correlation (rC), and residual correlation (rE). For more detail on the common factors bivariate model, see the supplementary materials. These analysis has previously been used to test for genetic correlation between facial traits (Lee et al., 2014, 2016). All analyses were conducted in OpenMx package in the R statistical software (Boker et al., 2011).

207 Results

Facial Trustworthiness

Visualisation of shape differences in trustworthiness are shown in Figure 2. A key area that appears to influence trustworthiness judgements in our sample is the shape of the mouth, with upturns in the corners of the mouth being associated with trustworthiness (i.e., a smile). This is inline with previous work that suggests subtle cues to emotional states of happiness are associated with trustworthiness ratings.



Figure 2. Visualisations of low (left) and high (right) shape differences on facial trustworthiness (\pm 3 *SD* from the mean face shape).

There were significant differences between twins and siblings in means and variance for rated facial trustworthiness such that the siblings were rated as more trustworthy compared to twins $(\chi^2(2) = 6.44, p = .040 \text{ and } \chi^2(2) = 7.54, p = .023 \text{ for means and variances respectively});$ therefore, models were run with the estimated means for twins and siblings both equated and not equated.

This did not influence the pattern of results, so we report models where sibling means were equated to those of twins. We also found significant differences in covariance between men and women of the same zygosity ($\chi^2(2) = 10.52$, p = .005). Indeed, as indicated by the twin-pair correlations reported in Table 2, male twin pairs had smaller twin-pair correlations on facial trustworthiness compared to female twin-pairs of the same zygosity. As a result, we estimated separate parameters for males and females.

Twin-pair correlations for facial trustworthiness are reported in Table 2. The overall MZ twin pair correlation was significantly larger than the DZ twin pair correlation ($\chi^2(1) = 10.65$, p = .001), indicating a genetic influence on the trait. Variance components from the ACE model are presented in Table 3. For women, shared environmental sources had a larger influence than genetic sources, though variation in facial trustworthiness was not significant for either. For men, or when sexes are pooled, variation in facial trustworthiness was significantly attributable to genetic sources.

Table 2. Twin-Pair correlations (r and 95% CI) for facial trustworthiness.

Zygosity Group	Facial	
	Trustworthiness	
All identical twins	.42 [.29, .54]	
Identical female twins	.47 [.31, .64]	
Identical male twins	.34 [.13, .55]	
All non-identical twins	.26 [.15, .38]	
Non-identical female twins	.41 [.25, .62]	
Non-identical male twins	.05 [16, .28]	
Non-identical opposite-sex twins	.22 [.03, .43]	
All non-identical twins + siblings	.19 [.09, .29]	
Non-identical female twins + female siblings	.36 [.21, .50]	
Non-Identical Male Twins + male siblings	.03 [14, .22]	
Non-identical opposite-sex twins + opposite-sex siblings	.11 [04, .25]	

Table 3. Proportions of variance of facial trustworthiness accounted for by A (additive genetic), C (shared environmental), and E (residual) influences.

	Fa	acial Trustworthin	ness
	A	С	Е
Females	.18 [.00, .52]	.28 [.00, .49]	.54 [.42, .67]
Males	.27 [.05, .43]	.00 [.00, .18]	.73 [.52, .92]
Overall	.39 [.18, .49]	.00 [.00, .15]	.61 [.51, .71]

Trustworthiness and Attractiveness

Phenotypic correlations (controlling for the non-independence of twins) between facial trustworthiness and other facial traits are reported in Table 4. There was a significant phenotypic

correlation between ratings of trustworthiness and attractiveness for both males and females. In order to determine if facial trustworthiness and attractiveness share a genetic component, we ran a common factors bivariate model. In the sex-specific model, none of the genetic, shared environmental, or residual correlations were significant. However, when the sexes were analysed together, we found a significant correlation between genetic components of facial trustworthiness and facial attractiveness (rA = .42, 95% CI = .09, .70). There was no significant shared environmental correlation in the sex-pooled model $\chi^2(1) = 1.46$, p = .230. Full models are reported in the supplementary materials.

Table 4. Phenotypic correlations (and corresponding 95% CI) between all facial traits. Correlations for males (N = 718) are in the upper corner, while those for females (N = 602) are in the lower corner.

258 MALES N = 718

	Trustworthiness	Attractiveness	Objective	Perceived	fWHR
			Masculinity	Masculinity	
Trustworthiness		.26 [.18, .33]	19 [25,14]	25 [33,17]	20 [28,12]
Attractiveness	.34 [.27, .41]		02 [11, .06]	17 [25,08]	12 [20,05]
Objective Masculinity	22 [30,14]	21 [28,13]		.21 [.13, .28]	11 [19,03]
Perceived Masculinity	30 [37,23]	69 [73,65]	.28 [.21, .35]		05 [13, .03]
Width-to-height ratio	12 [20,05]	06 [14, .01]	07 [15, .01]	03 [11, .04]	

FEMALES N = 602

Trustworthiness and Masculinity

Phenotypic correlations between facial trustworthiness and all three masculinity measures are reported in Table 4. For both men and women, there was a significant negative correlation between facial trustworthiness and both rated masculinity and objective masculinity. fWHR (purportedly representing a masculine facial trait) was also, to a lesser extent, significantly

negatively associated with trustworthiness ratings, but there was no significant positive correlation between perceived masculinity and fWHR in either men or women, or between objective masculinity and fWHR for women. There was a significant negative association between objective masculinity and fWHR in men, but this is the opposite direction to what would be expected if fWHR reflected masculinity as per the assumption in prior research. Indeed, women in our sample had significantly wider faces compared to men t(1227) = 2.45, p = .014. Together, these results further discredit fWHR as an appropriate index of masculinity.

As with facial attractiveness, we conducted common factors bivariate models with facial trustworthiness and each facial masculinity measure. Similar to the results for facial attractiveness, no genetic or shared environmental correlations were significant in the sex-specific models, with the exception of a significant genetic correlation between rated masculinity and facial trustworthiness in men. When considering sex-pooled models, results were inconsistent across the different masculinity measures. For the model with objective masculinity, there was no significant genetic correlation between facial trustworthiness and the objective masculinity score (rA = -.35, 95% CI = -.77, .10). However, there was a significant overall genetic correlation in the models that included rated masculinity (rA = -.50, 95% CI = -.75, -.30) and fWHR (rA = -.28, 95% CI = -.70, -.02). The C correlation was not significant in any of the sex-pooled masculinity models. Full models are reported in the supplementary materials.

285 Discussion

Overall, our results suggest that stable facial traits may be important when making trustworthiness judgements. We found a significant genetic component of facial trustworthiness in men and in the overall sample, and significant genetic correlations with stable morphological facial traits such as attractiveness, perceived masculinity, and fWHR. However, there was no significant

genetic or shared environmental correlation between facial trustworthiness and objective masculinity, despite there being a significant phenotypic correlation.

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When estimating parameters for each sex separately, neither genetic nor shared environmental sources significantly explain variation in facial trustworthiness for women. This likely due to a lack of power to adequately detect a significant effect, as the familial effect (i.e. genetic plus shared environment) is significant in both sexes, and also the genetic component by itself is significant when sexes are pooled. For nonidentical female twins, the twin-pair correlation was similar to that of identical twins, while virtually no correlation in facial trustworthiness existed between nonidentical male twins. This could suggest that genetic sources play a more important role in determining facial trustworthiness in men, but common environmental sources are more important in women. Indeed, we found that there was a significant genetic component of facial trustworthiness for men. This is consistent with previous research that has implied that making judgements of trustworthiness based on stable facial traits is particularly important in male targets (e.g., Stirrat & Perrett, 2010). Inaccurate trustworthiness judgements of men potentially carry higher costs compared to judgements of women in several contexts. For instance, when considering a mate, women overall face higher potential costs with choosing an untrustworthy partner due to minimal parental investment (Gangestad & Simpson, 2000). Also, trusting an untrustworthy male introduces higher physical risk, as men are more likely to have higher levels of aggression and strength (Zaatari & Trivers, 2007).

For both men and women, we found a significant positive phenotypic correlation between facial attractiveness and perceived trustworthiness, consistent with previous research (Langlois et al., 2000; Zaidel et al., 2003). We also contributed the novel finding that genetic sources associated with facial trustworthiness are also associated with facial attractiveness. If perceived trustworthiness reflected actual trustworthiness, this would support the evolutionary model where genes that influence facial trustworthiness are also found attractive since it is advantageous to choose a trustworthy mate for long-term relationships (Gangestad & Simpson, 2000). However,

given previous work has found a negative association between actual trustworthiness and attractiveness (Muñoz-Reyes et al., 2014; Shinada & Tamagishi, 2014; Takahashi et al., 2006; Zaatari & Trivers, 2007), the positive association between perceived trustworthiness and attractiveness more likely reflects a halo effect (Maestripieri et al., 2017). One might expect that any perceptible stable trait associated with untrustworthiness would be selected against, but such an association could evolve if the stable trait is highly desirable or advantageous in another domain (Haselhuhn & Wong, 2011). In a mating context, having a facially attractive partner is advantageous in various domains, such as potential genetic benefits to offspring health (Rhodes et al., 2001). As a result, there may be a positive net benefit in choosing an attractive partner despite them being less trustworthy; this may motivate individuals to in fact over-estimate positive attributes of facially attractive individuals (Maestripieri et al., 2017).

We also found a significant negative phenotypic correlation between facial trustworthiness and all three masculinity measures. This is consistent with previous findings that perceived facial masculinity is negatively associated with facial trustworthiness (Oosterhof & Todorov, 2008), and is the first demonstration of a significant association between trustworthiness and an objective facial masculinity score. Such a score entirely avoids the issue of fWHR not representing a sexually dimorphic trait (Kramer, 2017; Kramer et al., 2012; Lefevre et al., 2012; Özener, 2012).

Interestingly, the association between perceived facial trustworthiness and fWHR in our data is in line with previous found association between actual trustworthiness and fWHR (Haselhuhn & Wong, 2011; Stirrat & Perrett, 2010). Given that fWHR does not reflect masculinity, it is theoretically unclear why wide faces are seen as less trustworthy. We also found the association between trustworthiness judgements and masculinity with both men and women. Given that previous work investigating actual trustworthiness and facial attributes has focused on men (e.g., Haselhuhn & Wong, 2011; Stirrat & Perrett, 2010), our results indicate that future investigation should also consider women.

Bivariate quantitative genetic models including facial trustworthiness and masculinity were inconsistent between masculinity measures. While models that included either rated masculinity or fWHR revealed that these traits had a significant shared genetic component with facial trustworthiness, this genetic association was not significant for objective masculinity (though it was in the same direction). Previous work has theorised that sexually dimorphic men are less likely to be cooperative as they have an advantage in situations requiring physical strength and aggression (Stirrat & Perrett, 2010; Zaatari & Trivers, 2007). Our data suggests that this may also be reflected in trustworthiness judgements, but given the inconsistent results further investigation is needed.

While we focus the discussion on the influence of stable facial cues on trustworthiness judgements, our data does not exclude the possibility that dynamic cues are also important. Indeed, landmark configurations between trustworthy and untrustworthy faces suggest highly dynamic areas, such as the mouth, are important with trustworthiness judgements. In particular, upturned corners of the mouth were associated with greater trustworthiness ratings, lending support to the notion that trustworthiness judgements are influenced by emotional expression (Oosterhof & Todorov, 2009; Verplaetse et al., 2007), or may represent overgeneralisations of emotional state (Todorov, 2008).

Limitations of our study include those inherent to the classical twin design. This includes the inability to simultaneously estimate shared environmental (C) and non-additive genetic (D) variance, which may be particularly useful given the inconsistencies in twin-pair correlations for facial trustworthiness between non-identical men and women. This could be overcome by including other family members (e.g., parents) in the analysis. Also, previous research has indicated that there is high consensus in trustworthiness judgements (Zebrowitz et al., 1996), but there was comparatively low inter-rater consistency in our sample. Previous research has found that trustworthiness judgements are influenced by conditions of the perceiver, such as family composition (DeBruine et al., 2011), self-resemblance with the target (DeBruine, 2005), or sex (Wincenciak, Dzhelyova, Perrett, & Barraclough, 2013). Our analyses do not account for individual

differences in ratings of facial trustworthiness judgements, which could help explain the relatively low levels of inter-rater consistency for ratings of facial trustworthiness. Heritability estimates can be no more than the Cronbach's alpha because error contributes to the residual variance; therefore, improving the inter-rater consistency of facial trustworthiness may lead to higher heritability estimates. We could also expect that low consistency of facial trustworthiness judgements between raters would introduce noise to the analysis and reduce any detectable association between facial trustworthiness and other facial attribute.

Overall, our data suggests that both dynamic and stable cues may influence facial trustworthiness judgements. We note that here we solely investigate whether perceptions of trustworthiness are correlated with facial traits, and do not investigate the accuracy of those perceptions. Future research could investigate the association between facial characteristics and objective measures of trustworthiness, such as choices in economic games.

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