

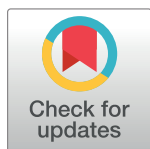
PERSPECTIVE

# Genes influence facial attractiveness through intricate biological relationships

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In Greek mythology, Helen of Troy was so beautiful that her face “launched a thousand ships,” compelling King Menelaus to wage war to reclaim her from Prince Paris. Human preoccupations with beauty are enduring and now support a multibillion-dollar industry. Each day, our brains identify and catalog innumerable datapoints that bear on our impressions of beauty—those related to youth, health, adiposity, complexion, coloration, averageness, symmetry, masculinity/femininity, and personality, to name some of the best characterized (Fig 1) [1]. Congruent with the common saying that “beauty is in the eye of the beholder,” perceptions of attractiveness vary within and among individuals and across cultures. Yet when multiple individuals compare the same set of faces, clear agreement exists both within and between cultures about which faces are most attractive.

Evolutionary hypotheses concerning the importance of attractiveness and its component factors in mate choice have revolved around the utility of these components in predicting the qualities of prospective mates [1]. For example, preferences for youthful appearance in female faces may function to direct courtship efforts toward those with high reproductive potential. Complexion and adiposity may reflect current health [2,3]. Other traits are purported to represent cues of underlying genes that increase the survival and reproduction of offspring by, for example, providing pathogen resistance, attractiveness, or dominance. Symmetry, masculinity, weight, and averageness have each been linked with indicators of genetic quality [3–5], though many of these relationships are contested [6–8].

## Genetics of facial attractiveness

Given the importance of attractiveness across interpersonal contexts, studies that investigate the underlying genetics of facial attractiveness, such as the one reported by Hu and colleagues [9] in this issue, are invaluable but should be interpreted carefully, commensurate with the complexity of attractiveness as a phenotype. Although Hu and colleagues report considerably lower heritability estimates for facial attractiveness than a previous estimate [10], perhaps due to modest interrater reliability (S13 Fig in [9]), evidence of heritability suggests that searches for underlying loci associated with attractiveness may bear fruit. Datasets with genome-wide genetic data and rated facial attractiveness are rare and time-consuming to gather, and Hu and colleagues smartly leverage a large, pre-existing dataset. After testing 6 overlapping sets of facial attractiveness ratings, they find 1 SNP associated with rated facial attractiveness at a study-wide threshold, 1 SNP significant at genome-wide threshold, and 10 suggestively significant SNPs.

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**Fig 1. Some well-characterized features influencing perceptions of facial attractiveness.** Depicted are physical traits that influence facial attractiveness through changes in shape (e.g., adiposity, averageness, masculinity/femininity, and symmetry) or color (e.g., complexion), as well as qualities influencing facial attractiveness that might also be inferred from both shape and color information (e.g., youthfulness, health, and personality). Relationships between each of these features and attractiveness are likely mediated by a host of biological factors influenced by genotype.

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Through a series of enrichment tests, Hu and colleagues identify several correlations between attractiveness ratings and genes influencing other traits—namely, body mass index in females and lipid traits in males (Fig 4 in [9]). Indeed, this study manifests as an illustration of the ability of a large GWAS on a complex phenotype to identify genes related to its simpler component traits and correlates. The candidate genes identified for both significant results and nearly all suggestive results have entries in GWAS Catalog for traits related to attractiveness, including skin pigmentation and melanoma, body mass index (BMI), and the BMI-related phenotypes of height and waist–hip ratio (Table 1). Homogeneous skin coloration [11] and red and yellow tints [12] increase ratings of attractiveness cross-culturally, potentially due to the connection between these traits and perceptions of health and youth. The relationship between weight and attractiveness is demographically variable; for example, American men of European descent rate lower weights as more attractive, except in extremely low BMI ranges [13], whereas African American men are more likely to prefer heavier figures [14]. Hu and colleagues also identify candidate genes related to attractiveness that have been previously associated with facial morphology, possibly implicating facial traits (such as those contributing to

**Table 1. GWAS results related to attractiveness.** Associations between genes identified in [9] and prior results related to attractiveness, found by searching GWAS Catalog (<https://www.ebi.ac.uk/gwas/>) for the candidate genes identified in [9] and selecting those results related to morphology, traits that influence attractiveness ratings, and the lipid traits described in [9].

Hu and colleagues		GWAS Catalog				
Trait	Candidate Gene	Trait	SNP	Candidate Gene	P-value	Study accession
MC-AS	<i>LRP1B</i>	Aging	rs12474609	<i>LRP1B</i>	6.00 x 10 <sup>-9</sup>	GCST000378
		Age at menarche	rs12472911	<i>LRP1B</i>	2.00 x 10 <sup>-7</sup>	GCST000880 GCST002541
		Body mass index	rs12617004	<i>LRP1B</i>	6.00 x 10 <sup>-9</sup>	GCST004904
	<i>PTPRT</i>	Facial morphology (factor 20)	rs2867028	<i>PTPRT</i>	4.00 x 10 <sup>-6</sup>	GCST004324
		Eye morphology (Left eye angle of en-ps-ex)	rs6016745	<i>PTPRT</i>	6.00 x 10 <sup>-6</sup>	GCST006105
		Obese body mass index	rs7263077	<i>PTPRT</i>	6.00 x 10 <sup>-6</sup>	GCST002828
FC-AS	<i>LY86</i>	Obese body mass index	rs4246076	<i>LY86, LY86-AS1</i>	6.00 x 10 <sup>-6</sup>	GCST002829
		Waist-hip ratio	rs1294421	<i>LOC101928004</i>	7.00 x 10 <sup>-14</sup>	GCST004064
						GCST000829
	<i>ANTXRPL1</i>	Melanin index	rs111256285	<i>ANTXRPL1</i>	8.61 x 10 <sup>-6</sup>	GCST004219
MC-FS	<i>CDC42EP3</i>	Facial morphology (factor 5, width of mouth relative to central midface)	rs116711337	<i>LOC107985870</i>	4.00 x 10 <sup>-6</sup>	GCST004309
		Height	rs17511102	<i>LOC105374465</i>	2.00 x 10 <sup>-18</sup>	GCST000817 GCST001956
	<i>SPON1</i>	Facial morphology (factor 1, breadth of lateral portion of upper face)	rs79756450	<i>LOC101928132, SPON1</i>	6.00 x 10 <sup>-7</sup>	GCST004328
FC-FS	<i>MED30, EXT1</i>	Obese body mass index status	rs3115775	<i>LOC105375721</i>	8.00 x 10 <sup>-6</sup>	GCST002828
		Height	rs1198912	<i>EXT1</i>	6.00 x 10 <sup>-6</sup>	GCST000522
		Cortisol secretion	rs7459527	<i>EXT1</i>	2.00 x 10 <sup>-6</sup>	GCST001762
	<i>NXN</i>	Facial morphology (factor 15, philtrum width)	rs3851779	<i>NXN</i>	4.00 x 10 <sup>-6</sup>	GCST004319
		Mean arterial pressure	rs747685	<i>NXN</i>	6.00 x 10 <sup>-7</sup>	GCST002497
		Diastolic blood pressure	rs747687	<i>NXN</i>	2.00 x 10 <sup>-7</sup>	GCST002497
MC-MS	<i>RAB11FIP4</i>	-	-	-	-	-
FC-MS	<i>CERS2, ANXA9</i>	High density lipoprotein cholesterol measurement	rs267738	<i>CERS2</i>	6.00 x 10 <sup>-12</sup>	GCST006611
		Low density lipoprotein cholesterol measurement	rs267733	<i>ANXA9</i>	4.00 x 10 <sup>-8</sup>	GCST004233
						GCST002222
	Melanoma	rs1722784	<i>ANXA9</i>	2.00 x 10 <sup>-6</sup>	GCST001245	
	<i>LOC285692</i>	-	-	-	-	-
	<i>PDZRN4, GXYLT1</i>	Height	rs1405552	<i>PDZRN4</i>	1.00 x 10 <sup>-10</sup>	GCST005951 GCST006368
		Skin pigmentation	rs1902910	<i>PDZRN4</i>	2.00 x 10 <sup>-6</sup>	GCST004219
		Height	rs285575	<i>PDZRN4</i>	7.00 x 10 <sup>-8</sup>	GCST002783
		Overweight body mass index	rs11180992	<i>PDZRN4</i>	3.00 x 10 <sup>-6</sup>	GCST002829
Height		rs11181001	<i>PDZRN4</i>	4.00 x 10 <sup>-10</sup>	GCST005951 GCST006368	
Diastolic blood pressure		rs7965392	<i>GXYLT1, YAF2</i>	4.00 x 10 <sup>-10</sup>	GCST006627	

Note: Candidate genes with significant results in [9] are bolded. P-value refers to the P-value in the GWAS catalog study, represented by the GWAS catalog study accession number. AS, all samples; FC, female coders; FS, female samples; GWAS, genome-wide association study; MC, male coders; MS, male samples.

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youthful facial appearance) in perceptions of attractiveness [15]. One explanation for Hu and colleagues finding a genetic association between male-rated female attractiveness and BMI is a mediating relationship whereby the candidate gene (*CDC42EP3*) affects height, which directly influences BMI. Similarly, the genetic association between female-rated male attractiveness and lipid levels observed by Hu and colleagues could be explained by the previously identified impact of candidate genes *CERS2* and *ANXA9* on both high- and low-density lipoprotein cholesterol levels (Table 1). It is also possible that Hu and colleagues find different loci for male- and female-rated attractiveness because men and women seem to vary in the specific traits they perceive as attractive [16].

## The future

The results of this study point to underlying genetic architecture mediating attractiveness. In the future, careful multivariate studies testing the relative contribution of each associated locus to the component traits of attractiveness, and to attractiveness corrected for those traits, will help researchers unravel and interpret the genetic architecture of this important and complex phenotype. Of course, replication in the few other datasets possessing both genotype and attractiveness data will aid in validation and resolution of these results, and sequencing studies will help clarify the possibly functional variants at each locus and further explore their effect on attractiveness or its related components. Hu and colleagues also briefly mention signatures of selection on alleles associated with male facial attractiveness. This result is especially intriguing and brings up several avenues for future research. Do other secondary sex traits, such as vocal characteristics, show similar signatures of selection in males, indicating sexual selection among our male ancestors [17]? Importantly, does the selection pressure driving the strong relationship between allele frequency and male attractiveness reflect pressure upon the attractiveness per se, or upon related phenotypes, such as lipid metabolism? How do potential signatures of selection fit in with previous evolutionary hypotheses? If there are causative pathways between the associated loci and attractiveness, have cross-cultural variations in preference [18] led to population-specific allele variation at these candidate attractiveness loci?

When contemplating how to depict Helen of Troy, the 5th century BC painter Zeuxis recognized the challenge of identifying the features that define beauty [19]. This challenge remains, and understanding the biological factors that influence attractiveness is equally compelling and complex. Hu and colleagues bring forth a valuable initial foray into the genetic architecture of attractiveness and emphasize the intricate relationships between attractiveness and other visible traits.

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