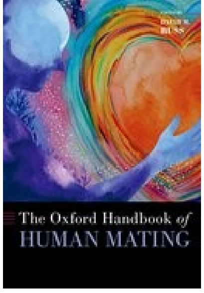

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CHAPTER

7 The Logic of Physical Attractiveness: What People Find Attractive, When, and Why

David M. G. Lewis, Kortnee C. Evans, Laith Al-Shawaf

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Abstract

Attractiveness is a perception produced by psychological mechanisms in the mind of the perceiver. Understanding attractiveness therefore requires an understanding of these mechanisms. This includes the selection pressures that shaped them and their resulting information-processing architecture, including the cues they attend to and the context-dependent manner in which they respond to those cues. We review a diverse array of fitness-relevant cues along with evidence that the human mind processes these cues when making attractiveness judgments. For some of these cues, there is unequivocal evidence that the cue influences attractiveness judgments, but exactly *why* attractiveness-assessment mechanisms track that cue is an area of current debate. Another area of active inquiry is *when* these cues influence attractiveness judgments: because the fitness costs and benefits associated with these cues would have varied across contexts, selection should have shaped attractiveness-assessment mechanisms to be sensitive to contextual variables. As a consequence of this context-sensitive design, these mechanisms, despite being universal, should produce attractiveness assessments that vary systematically and predictably across contexts. We review evidence indicating that this is how human perception of attractiveness works, and highlight the need for more comprehensive and systematic investigations into contextual variation in human standards of attractiveness. We conclude by identifying limitations on existing evolutionary research on attractiveness, and provide concrete suggestions for how future work can address these issues.

Keywords: physical attractiveness, evolutionary psychology, mate preferences, waist-to-hip ratio, fluctuating asymmetry

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Attractiveness is not an inherent property of the entity being perceived; it is a perception produced by psychological mechanisms in the mind of the perceiver. Understanding attractiveness therefore requires an understanding of these mechanisms. This includes their causal origins—the selection pressures that shaped them—and the resulting design of their information-processing architecture, including the specific cues they attend to and their sensitivity to contextual variables.

In this chapter, we first identify what attractiveness is and what perceptions of it do. The motivational consequences of perceiving another individual as attractive provide key ↳ insight into why evolution by natural selection would have shaped these mechanisms in the first place: to guide people toward fitness-enhancing selection of relationship partners.

We review a diverse array of these fitness-relevant cues and the empirical evidence demonstrating that the human mind regulates its perceptions of potential mates' attractiveness in response to them. For some cues, it is clear *whether* they influence perceptions of attractiveness, but the precise evolutionary reason *why* attractiveness-assessment mechanisms track that cue is an area of current debate. Another area of active inquiry is *when* these cues influence perceptions of attractiveness—the fitness costs and benefits of the traits indicated by the cues would have varied across contexts, so selection should have shaped attractiveness-assessment mechanisms to be sensitive to these contextual variables. Because of this context-sensitive design, these mechanisms should produce attractiveness assessments that vary systematically and predictably across different contexts. We review evidence suggesting that this is how these mechanisms operate, and highlight the need for more comprehensive and systematic investigations into cross-context variation in human standards of attractiveness.

We then briefly contextualize these empirical findings and theoretical ideas in the broader landscape of interpersonal attraction. This chapter focuses on the perception of attractiveness in response to cues that are (1) morphological, (2) visually observable, and (3) of fitness relevance for mating relationships. Humans' broader psychology of interpersonal attraction also includes cues that are dynamic (i.e., movement-based), detectable via nonvisual modalities (e.g., olfaction, audition), and relevant to nonmating relationships (e.g., kin-based relationships, friendships, coalitions). Although it is beyond the scope of the current chapter to cover this entire landscape, the principles and evolutionary logic that we outline here apply across different classes of cues, across the different perceptual modalities by which they are detected, and across human relationship types.

Finally, we conclude by identifying significant limitations on existing evolutionary research on attractiveness, and provide concrete suggestions for future work to address these issues.

Attractiveness as Perception

Attractiveness is commonly attributed to the perceived entity itself: "that flower is beautiful," "that man is unattractive." However, attractiveness is not a property of the object being perceived, but rather is a perception produced by psychological mechanisms in the mind of the perceiver.

This important distinction is illustrated well by humans' aversion to—and houseflies' affinity for—the volatized chemical compounds emitted from feces. When olfactory receptor cells bind to these chemical compounds, they initiate a relay of electrical and chemical messages that results—for humans—in the perception of an unpleasant smell, a feeling of disgust, and avoidance of the source of the odorants (Rozin & Fallon, 1987). For flies (e.g., the common housefly, *Musca domestica,* or its close relative *Musca sorbens*), p. 180 ↳ the same chemical compounds evoke a diametric set of motivational and behavioral outcomes (Robinson et al., 2020). The fact that feces can be both attractive (to houseflies) and unattractive (to humans) underscores that attractiveness is not a property of the perceived entity but rather a perception produced by mechanisms in the mind of the perceiver. Understanding attractiveness therefore requires an understanding of these mechanisms.

First, we must understand their causal origins. Because evolution by natural selection is the only known causal process capable of producing complex organic mechanisms, an understanding of these mechanisms requires an understanding of the selective pressures that shaped them.

The Selective Origins of Attractiveness-Assessment Mechanisms

Our example of feces, houseflies, and humans also illustrates *why* selection fashioned psychological mechanisms that produce perceptions of attractiveness. Imagine a world in which houseflies do *not* exhibit any affinity for feces. Let us introduce into that world a “mutant” housefly that is equipped with cognitive (i.e., information-processing) machinery that, in response to detecting cues to presence of feces, motivates approach behavior toward their source. Because feces are a valuable source of nutrition for housefly larval development—because feces *helped* houseflies solve an adaptive problem recurrently faced during their species’ evolution (Robinson et al., 2020)—mutant houseflies would enjoy greater fitness than their counterparts who were not attracted to feces. This greater fitness of the mutant housefly means that the proportion of houseflies with this cognitive machinery would increase in the population in each subsequent generation until the entire population consisted of mutant houseflies: the information-processing mechanisms responsible for detecting cues to feces and motivating approach would become a universal component of housefly nature.

For humans, on the other hand, feces are a source of disease; they *cause* an adaptive problem (Cosmides & Tooby, 1997). Consequently, we should expect humans to possess psychological mechanisms to detect and process cues to the presence of feces, but with design features that are opposite to those observed in flies. Ancestral humans who possessed psychological mechanisms that responded to cues to feces with subjective states motivating avoidance behavior would have experienced greater fitness than individuals who lacked these mechanisms.

This is why selection shaped mechanisms in both houseflies and humans to detect volatilized chemical compounds that cue the presence of feces, but with different design features: in houseflies, the mechanism motivates approach in response to cues to feces, whereas humans’ mechanism produces subjective states, such as repulsion and a feeling of disgust, that instead motivate avoidance (Cosmides & Tooby, 1997).

The same evolutionary logic applies to the information-processing mechanisms responsible for perceiving another individual as attractive. Ancestral humans who possessed psychological mechanisms that (1) attended to cues in a potential mate that were predictive of positive fitness consequences of mating with that individual and (2) generated preferences for mates exhibiting these cues would have outreproduced their counterparts who lacked such mechanisms. Because the individuals with these psychological mechanisms would have enjoyed greater fitness, the proportion of the population that possessed this cognitive machinery would have increased iteratively across generations until these information-processing mechanisms became a universal component of human nature.

The selective origins of these mechanisms have key implications for their information-processing design. Selection shaped these mechanisms to attend to cues in a potential mate that were ancestrally predictive of the fitness consequences of mating with that individual (henceforth, the cue’s *fitness value*). This is the first key design feature of attractiveness-assessment mechanisms: selection shaped them to attend and respond to cues that were relevant to reproductive fitness.

However, the fitness value of a cue would have varied across contexts. For example, the fitness value of a cue to immediate fertility is greater in the context of short-term mating than in the context of long-term mating; a conspecific’s immediate fertility may be paramount for reaping fitness benefits from a single act of sexual intercourse, but largely irrelevant to the fitness consequences of selecting that individual as a long-term mate. The opposite is true of cues to future reproductive potential; cues to future reproductive potential may be paramount in long-term mating but largely irrelevant to short-term mating (see Goetz et al., 2012, for dozens of cues hypothesized to predict different fitness consequences in short-term vs. long-term mating). The broader point is that, because the fitness value of a cue systematically depends on specific contextual variables, selection should have shaped attractiveness-assessment mechanisms to be sensitive to these contextual variables. This is important because it means that, despite the universality of these psychological mechanisms, they should produce systematic variation in what people find attractive across contexts, including across cultures.

Whether, *Why*, and *When*: Three Interrelated but Distinct Questions

In the following sections, we discuss how attractiveness-assessment mechanisms regulate attractiveness perceptions in response to (1) cues ancestrally predictive of the fitness consequences of mating with a particular individual and (2) contextual variables that shift the fitness value of those cues.

We approach this task in a manner that differs from previous literature. Previous work in this domain (e.g., Sugiyama, 2015) has interwoven evidence that the mind tracks a cue (which answers the question of *whether* attractiveness-assessment mechanisms track that cue) with proposed explanations for *why* they track that cue, with documented or hypothesized variation in how the mechanism responds to that cue across contexts (*when*). Our primary reason for addressing these three issues separately is that existing answers to these ↳ three questions have very different statuses. In some cases, decades of empirical research have demonstrated robust effects of a cue on perceptions of attractiveness, but uncertainty remains about which existing hypothesis, if any, correctly accounts for why this cue is important. These divergent statuses of *whether* and *why* may reflect an underspecification of hypotheses. Later, we discuss this issue at greater length and make specific recommendations for how to resolve it. Nonetheless, the current state of knowledge is such that, for many cues, answers to *whether* attractiveness-assessment mechanisms track them and *why* they do are characterized by very different levels of certainty. It therefore makes sense to address these questions separately.

Why Specific Cues Should Influence Attractiveness, and *Whether* They Do

For each cue discussed below, we outline *why* selection might have shaped psychological mechanisms to attend to that cue: what fitness-related trait or traits appear to be linked to that phenotypic cue? We attempt to highlight, where appropriate, the tentative nature of claims about the fitness implications of the cue. In some cases, robust empirical links exist between cues and fitness-relevant outcomes. In other cases, the link between a cue and fitness-relevant outcomes may only be hypothesized, or the cue may exhibit a tenuous empirical relationship to a fitness-relevant outcome—or doubt has been cast by recent work on a link that was once regarded as robust.

After addressing the *why*, we address *whether* attractiveness-assessment mechanisms track these cues. By and large, the corpus of empirical literature indicates that attractiveness-assessment mechanisms do track these cues. However, recent developments that have occurred in association with the movement in psychological science toward more open, preregistered science and the publication of null results suggest that some of these links may be less reliable and weaker than once thought. We attempt to balance discussion between the accumulated corpus of literature with recent concerns about some historically influential claims.

Symmetry

Many developmental programs are designed to produce bilaterally symmetrical features: right and left eyes that are the same size and shape—and at the same height on the face, a nose that aligns with the midline of the face and has equal-sized right and left sides, and legs of the same length. Deviations from bilateral symmetry in these features have been hypothesized to cue developmental instability, reflect mutational load or deleterious homozygosity, and be associated with lower levels of fitness (see Van Dongen, 2006, 2016, for review).

Links between symmetry and fitness-related outcomes have been documented in both nonhuman animals and humans. Research on nonhuman animals has documented links between symmetry and a diverse range of these outcomes, from growth and survival to fecundity and mating success (see Van Dongen, 2006). Research on humans has reported ↳ associations between symmetry and similarly diverse fitness-linked variables. For example, Waynforth (1998) showed that greater symmetry was associated with lower morbidity and greater fecundity among Mayan men in rural Belize. In WEIRD (Western, educated, industrialized, rich, and democratic) populations with lower levels of exposure to pathogens, resource scarcity, and other environmental stressors, some of the associations between symmetry and health may be attenuated or absent (e.g., see Pound et al., 2014). In these environments, symmetry nonetheless appears to be positively associated with IQ (Pound et al., 2014) and meta-analyses indicate a small but positive correlation between symmetry and general mental ability (range for estimate of population-level correlation: 0.12–0.20, see Banks et al., 2010). Low levels of symmetry have also been linked to the development of schizophrenia, and, among schizophrenics, those who exhibit greater asymmetry experience earlier onset of the disease and suffer from greater disease severity (Markow & Wandler, 1986).

The reliability and robustness of these links, however, is an area of active debate. Studies investigating associations between symmetry and fitness in nonhuman taxa have exhibited a great deal of heterogeneity, and, in humans, the strength of association between symmetry and various fitness-related outcomes has differed substantially across studies. Although the mean documented effect size is approximately 0.2, study-specific effect sizes have ranged widely—from *negative* 0.2 to 1.0—and have been inversely related to sample size. These issues raise concerns about publication bias and the reproducibility of these reported symmetry–fitness links (see Van Dongen & Gangestad, 2011; Van Dongen, 2016). Nonetheless, available evidence suggests that, at least in some cases, symmetry can cue genetic quality and exposure to environmental stressors during development (Van Dongen, 2016). For example, symmetry reliably tracks developmental stability in cases of substantial ontogenetic insult (e.g., Bots et al., 2014; Woolf & Gianas, 1977), and the harsher ecological conditions experienced by foraging populations are associated with higher mean population-level asymmetry than that observed in WEIRD populations (Gray & Marlowe, 2002). This may be an important piece of the puzzle: variation in symmetry may not reliably track individual quality in WEIRD societies, but it may reliably track individual quality in environments that more closely approximate the conditions in which our species evolved. Future research is needed to map the conditions in which symmetry reliably predicts fitness-relevant outcomes, but if the observed symmetry–fitness associations held under ancestral conditions, then selection should have shaped attractiveness-assessment mechanisms to attend to symmetry.

Numerous studies report findings consistent with this hypothesis. People perceive more symmetrical faces —both male and female—to be more attractive (e.g., Rhodes, 2006). People with more symmetrical bodies —from college students to villagers in Dominica—are rated as more attractive (Brown et al., 2008; Hume & Montgomerie, 2001; Thornhill & Gangestad, 1994). Individuals with more symmetrical bodies report having sex earlier in life (Thornhill & Gangestad, 1994) and a greater number of sexual affair partners ↳ (Gangestad & Thornhill, 1997), copulations with mated individuals (Gangestad & Thornhill, 1997), and lifetime sexual partners (Thornhill & Gangestad, 1994). Van Dongen and Gangestad's (2011) meta-analysis of nearly one hundred studies involving close to 50,000 participants revealed robust, though small, statistical associations (1) between symmetry and multiple broad categories of fitness-related outcomes, from health to psychological maladaptation, and (2) between symmetry and perceptions of attractiveness.

These findings suggest that the human mind possesses psychological mechanisms to track symmetry and regulate perceptions of attractiveness in response to it. However, several important concerns have been raised in recent literature about the reproducibility of reported symmetry–attractiveness links. First, multiple studies have found no such effect (e.g., Jones & Jaeger, 2019; Weiss et al., 2020). Second, symmetry–attractiveness relationships appear to be highly sensitive to the method and measurements employed. Compared to studies that measure naturally occurring variation in symmetry, studies that manipulate symmetry are statistically more powerful and thereby more likely to detect an effect—but they also may break up naturally occurring associations between symmetry and other hypothesized cues to individual quality (Van Dongen, 2016), which undermines the ecological validity of any reported effects. The effect of symmetry on social perceptions (e.g., attractiveness) also appears to be largely contingent on how symmetry is scored. Studies using the scoring method of Horizontal Fluctuating Asymmetry (HFA) appear to disproportionately report associations between symmetry and attractiveness (see Weiss et al., 2020). This raises flags because the other traditional scoring method—Horizontal Angular Asymmetry (HAA)—is arguably the purer measure of symmetry; unlike HFA, it is not sensitive to extrinsic factors (e.g., head roll or yaw, see Weiss et al., 2020). Even more strongly, Weiss et al. (2020) have shown that HFA may capture *only* these extrinsic factors and not be linked to intrinsic asymmetry at all. HAA is not free of issues, either, however. Of four distinct forms of intrinsic facial asymmetry, HAA fails to capture significant variance on two of these dimensions (see Weiss et al., 2020)—which calls into question any HAA-based claims that perceptions of attractiveness are *not* related to symmetry.

Clearly, superior measures of symmetry are needed, but it is not clear exactly what such a superior measure will look like—or, for that matter, whether measuring a single type of symmetry is appropriate. Weiss et al. (2020) have provided evidence that there are at least four distinct types of asymmetry in the face alone, and that the human mind tracks these different types of asymmetry independently. These findings raise concerns about using a single, composite measure of symmetry, as distinct types of symmetry may cue distinct information and have different effects on attractiveness perceptions. By using a single composite measure, these effects could be muddled or lost altogether: when Weiss et al. (2020) created an aggregate measure of facial asymmetry based on the four types of symmetry they identified, the aggregate measure failed to capture the effects that were exerted by the individual types independently.

p. 185 In sum, future work is needed to more conclusively test the hypothesis that symmetry is a fitness-relevant cue that influences perceptions of attractiveness. A key goal of future research should be to more clearly establish the precise conditions in which symmetry reliably cues developmental stability or other fitness-relevant variables. This information will be essential for researchers to generate theoretically anchored hypotheses about why, when, and how humans' attractiveness-assessment mechanisms track symmetry in the human phenotype.

Waist-to-Hip Ratio

The ratio of a woman's waist circumference to her hip circumference (waist-to-hip ratio, or WHR) has been hypothesized to be linked to myriad fitness-related variables—as many as forty-two, according to Bovet's systematic review (see Bovet, 2019, fig. 1, panel B). As Bovet (2019) points out, robust empirical links to WHR exist for fewer than half of these fitness-related outcomes, many of the fitness-related outcomes that are linked to high WHR are evolutionarily novel and pertain only to WEIRD societies (Eaton et al., 1997), and links between WHR and some of these outcomes have been documented predominantly among individuals over sixty—well beyond when most reproductively relevant mate choices would have occurred in ancestral conditions. These observations are valuable for ruling out specific hypotheses. However, they should not be interpreted to mean that WHR does not cue important fitness-related information: the best available evidence suggests that it does.

WHR appears to be a reliable cue to *parity*. The allocation of gluteofemoral fat deposits during pregnancy and lactation, coupled with the deposition of fat on the abdomen after the postpartum period, increases waist circumference relative to hip circumference. This results in WHR increasing with number of previous pregnancies, an observation that has been documented among human populations on all inhabited continents and in both WEIRD and nonindustrial societies (see, e.g., Butovskaya et al., 2017; Lassek & Gaulin; 2006).

Parity would have been a fitness-critical variable for two different reasons. First, due to women's finite reproductive resources, the *number* of future children that a woman can bear is inversely related to the number she has already borne. Second, the *quality* of future descendants is also influenced by parity: high parity is associated with both lower birthweight (e.g., Kiely et al., 1986) and lower IQ (i.e., later-born children have lower IQ than first-born children; see Rohrer et al., 2015), as well as with a reduced capacity to buffer fetal development against environmental stressors (Merklinger-Gruchala et al., 2017).

Future work is needed to further assess the plausibility of the (at least) seventeen other hypotheses for why selection should have shaped attractiveness-assessment mechanisms in men to attend to women's WHR (see Bovet, 2019). However, because of (1) the robust links between WHR and parity and (2) the relevance of parity for reproductive fitness, p. 186 ↳ selection should have shaped male psychological mechanisms to attend to women's WHR when producing attractiveness judgments.

A multitude of empirical studies employing diverse methods and drawing on numerous sources of data have shown that women's WHR does indeed influence men's perception of their attractiveness. This body of research has included studies employing methods ranging from simple line drawings (e.g., Singh, 1993a) to 3D body scans (Brown et al., 2008) to brain activity (e.g., Platek & Singh, 2010). It has also included the use of archival data, such as the WHRs of Miss America winners and Playboy playmates in the last century (Bovet & Raymond, 2015; Singh, 1993a), as well as the WHR of the idealized woman as depicted in Western artwork over the last 2,500 years (Bovet & Raymond, 2015). It also has included research demonstrating that congenitally blind men without any previous visual experience prefer a low WHR when assessing female body shape through touch—a preference that their sighted counterparts also exhibit (Karremans et al., 2010). So many studies have documented the influence of women's WHR on men's perceptions of their attractiveness that some authors refer to the number of studies that have *not* found such preferences: "Only three studies report no effect of WHR on attractiveness" (Sugiyama, 2015, p. 50). In these rare cases where no male preference for a specific female WHR was observed, the studies' stimulus sets included a very small number of stimuli, conflated WHR with other variables such as body weight, or both (see Sugiyama, 2015).

Follow-up studies (e.g., Sugiyama, 2004b; Tovée et al., 2006) that addressed these confounds showed that men's preferences for specific WHR values become clear when WHR is disentangled from confounds such as weight or body fat. Subsequently, Singh et al. (2010) cross-culturally demonstrated that WHR influences perceptions of attractiveness independent of body weight or body mass index (BMI). In their research, Singh and colleagues used stimuli that manipulated WHR but not BMI: they used pre- and postoperative photographs of women who had undergone micrograft surgery to remove fat from the abdomen and deposit it in the buttocks. Raters from four distinct cultures—Bakossiland in Cameroon, Komodo Island in Indonesia, New Zealand, and Samoa—judged the postoperative photos to be more attractive. In addition to these within-woman shifts in attractiveness predicted by their reduced WHR, between-woman variation in WHR also predicted perceptions of attractiveness in all four cultures. Finally, Platek and Singh (2010) showed that when men viewed the photos, the changes in WHR associated with the postoperative photos were associated with the activation of the anterior cingulate cortex, a region of the brain involved in reward and decision-making.

In short, there is an abundance of evidence that the male mind tracks women's WHR. Nonetheless, further work is needed to pin down precisely *why* selection shaped male psychological mechanisms to attend to women's WHR. The parity hypothesis appears to be the leading hypothesis for why men's attractiveness-assessment mechanisms attend to women's WHR. However, other hypotheses may overlap with this hypothesis ↳ (e.g., the hypothesis that WHR cues the quantity and availability of "reproductive fat"—see Singh, 1993b, and Bovet, 2019, for review), and yet others propose alternative, or additional, selection pressures for the evolution of male psychological mechanisms to attend to women's WHR.

For example, another hypothesis proposes that selection shaped male psychology to attend to women's WHR because it reliably cues *reproductive age*. Consistent with this hypothesis, an inverse relationship between women's WHR and age-linked reproductive capacity has been documented across numerous WEIRD and non-WEIRD populations: female WHR decreases with puberty and the onset of menarche, and then increases with age after peak fertility is reached (see Bovet, 2019, for review). This hypothesis is complicated, however, by the fact that age can be assessed through numerous other cues, ranging from skin and hair quality (see below) to breast development and other secondary sexual characteristics. Such cue redundancy can prevent the evolution of psychological systems to attend to a particular cue—even if that individual cue has the greatest predictive validity (see Iwasa & Pomiankowski, 1994). However, attending to and integrating redundant cues can reduce inferential errors (Johnstone, 1996). If the benefits of the increase in inferential accuracy outweigh the costs associated with the development and maintenance of neuropsychological systems to attend to and integrate redundant cues, selection can shape mechanisms that attend to multiple cues to the same underlying information (see Johnstone, 1996). Whether this is the case for WHR as a cue to reproductive age remains to be resolved.

In sum, the best evidence currently available suggests that the parity hypothesis is the most theoretically plausible and empirically compelling account for why male psychological systems attend to women's WHR and regulate attractiveness assessments in response to it. Nonetheless, we eagerly await further testing of this and more than a dozen other evolutionary hypotheses about the function of WHR-tracking mechanisms.

Androgen-Linked Features

Several hypotheses propose that androgen-linked traits in men, such as muscularity, height, and specific facial structures, may convey fitness-relevant information.

One broad hypothesis is the costly signaling hypothesis: that androgen-linked features are costly to develop, and therefore cue phenotypic and possibly genotypic quality. Within this costly signaling perspective, some research has proposed that testosterone has direct immunosuppressive effects and that androgen-linked features cue men's immunocompetence specifically (e.g., see Al-Shawaf et al., 2017; Thornhill & Gangestad, 2006). Other work suggests that these traits are a costly signal but for reasons not directly related to immunocompetence (e.g., see Kokko et al., 2003). For example, greater body size—whether because of greater height, muscle mass, or both—increases energy demands and reduces the capacity to allocate resources to other aspects of somatic upkeep and immune function (Buchanan et al., 2001; Salska et al., 2008).

p. 188 There is some, albeit limited, evidence suggesting an association between androgen-linked features and individual quality. This includes links to health-related variables such as respiratory disease duration (Thornhill & Gangestad, 2006) and hepatitis B vaccine antibody response (Skrinda et al., 2014), as well as to developmental stability. However, these links may be mediated by factors such as nutrition, lower exposure to pathogens, and greater access to resources during ontogeny (Perkins et al., 2016).

An alternative to the costly signaling hypothesis is that androgen-linked traits are associated with the ability to obtain and defend resources, including reproductively relevant resources via intrasexual mating competition (Puts, 2010; Puts et al., this volume; see also Caton & Lewis, 2021a, 2021b). Future research is needed to determine which of these is correct, if any. For now, it appears safe to conclude that at least some androgen-linked traits are associated with fitness-relevant outcomes. If this is correct, selection might have shaped psychological mechanisms in women's minds to track these cues and regulate perceptions of attractiveness in response to them.

Numerous studies suggest that women's attractiveness-assessment mechanisms track androgen-linked cues in men. Muscularity (Frederick & Haselton, 2007; Sell et al., 2017; see also Caton & Lewis, 2021b), androgen-linked facial features (DeBruine et al., 2010; Johnston et al., 2001), and height (Salska et al., 2008) all have demonstrated influences on women's perceptions of men's attractiveness. More muscular men also report more lifetime sexual partners, short-term sexual partners, and affairs with mated women (Frederick & Haselton, 2007), and taller men experience greater long-term mating success (see Pawlowski et al., 2000).

Other studies suggest that women perceive faces with *low* levels of androgen-linked features to be more attractive (e.g., Alharbi et al., 2020). Penton-Voak et al. (1999) proposed that variation in women's preferences for male facial masculinity may reflect a trade-off: the direct genetic benefits for offspring may only exceed the costs of lower investment from high-androgen men when women are likely to conceive. However, recent evidence suggests that female preferences for height and muscularity are linear and robust (Sell et al., 2017). These divergent results for (1) facial masculinity and (2) other androgen-linked features, such as muscularity, suggest that these distinct cues may not tap the same fitness-relevant dimensions. A recent meta-analysis corroborates this: all androgen-linked features *except* facial masculinity appear to be associated with greater mating success (Lidborg et al., 2021). Strength and muscularity were the strongest and most consistent predictors of outcomes relevant to mating success, which included indicators of outcompeting other men (i.e., intrasexual selection) as well as female mate choice (i.e., intersexual selection). We eagerly await the publication of this meta-analysis in a peer-refereed journal, as it could offer invaluable insight into (1) androgen-linked features as costly signals, cues to the ability to obtain and defend resources, or indicators of other fitness-relevant information; (2) whether different features, such as facial masculinity and muscularity, cue distinct dimensions of fitness-relevant information, and ↳ (3) p. 189
whether women's information-processing mechanisms respond differently to these distinct cues.

Lumbar Curvature

Women's lumbar spine is unique in the animal kingdom. As the only extant bipedal primates—and because men do not get pregnant—women are the only existing organisms that face the adaptive problem of a forward-shifting center-of-mass during pregnancy. Selection shaped a morphological adaptation to this problem: wedging in the third-to-last lumbar vertebra. This wedging is present in the spines of human females but absent from the spines of human males and both male and female quadrupedal primates (Whitcome et al., 2007), consistent with the fact that only female bipedal primates face the adaptive problem of an anteriorly shifted center-of-mass during pregnancy. Indeed, this wedging *is* present in the fossilized remains of females—but not males—of extinct bipedal hominin lineages (see Whitcome et al., 2007).

This morphological adaptation has critical fitness implications for women, their mates, their developing fetus, and any existing dependent offspring. Without this vertebral wedging, women's ability to shift the gravid center-of-mass would be dramatically impaired, and they could experience as much as an eightfold increase in hip torque during pregnancy (Whitcome et al., 2007). This would have resulted in protracted contraction of women's lower back muscles, resulting in muscular fatigue, increased risk of debilitating back injury, and impaired foraging ability (see Whitcome et al., 2007). Given that women provide a substantial number of calories to the family diet in traditional (e.g., forager) societies, a reduction in a woman’s foraging capacity could have subjected her, her mate, their developing fetus, and any existing offspring to malnutrition.

These consequences of women’s lumbar vertebral wedging set up selection pressures for the evolution of male psychological mechanisms to attend to cues of vertebral wedging. Women’s lumbar (lower back) curvature is a reliable, externally observable cue to this wedging (George et al., 2003). Based on this, we should expect selection to have favored male psychological mechanisms to attend to women’s lumbar curvature and regulate mating attraction accordingly. Too little vertebral wedging (hypolordosis) would have been associated with the inability to shift the gravid center-of-mass back over the hips, but *excessive* vertebral wedging (hyperlordosis) also carries fitness costs. Excessive wedging increases shearing forces that can lead to severe injuries such as herniated discs (see Whitcome et al., 2007). Consequently, selection should have favored male psychological mechanisms that produce the highest attractiveness judgments in response to an angle of lumbar curvature that cues the capacity to recenter the gravid center-of-mass over the hips but does not shade into excessive wedging and associated shearing forces on the spine.

Lewis et al. (2015) tested this hypothesis, now known as the *fetal load hypothesis* (see Lewis et al., 2021). The hypothesis proposes that men will be most attracted to an angle of lumbar curvature that minimizes the net p. 190 fitness costs of insufficient and excessive vertebral ↳ wedging, but it does not specify the value of this angle. Lewis et al. (2015) consulted the medical orthopedic literature to identify the angles of lumbar curvature associated with the fitness threats of hypolordosis and hyperlordosis. They predicted that men would prefer an angle of lumbar curvature maximally distant from these countervailing threats. According to the medical orthopedic literature, that angle is approximately 45.5° (see Fernand & Fox, 1985; Lewis et al., 2015). The researchers tested this proposed male preference by presenting men with images of opposite-sex morphs that systematically varied in their degree of lumbar curvature. Consistent with the fetal load hypothesis, men’s perceptions of women’s attractiveness peaked at approximately 45.5°—morphs with lumbar curvature values both below and above this value were perceived as less attractive. Subsequent work by Lewis and colleagues demonstrated that this preference cannot be attributed to a preference for greater buttock mass (see Lewis et al., 2015, Study 2); that high heels increase perceptions of women’s attractiveness only when donning them shifts women’s lumbar curvature closer to the proposed fetal load optimum (Lewis et al., 2017b); and that men track women’s angle of lumbar curvature even when presented with female stimuli that are in motion (Lewis et al., 2021).

Skin

As the natural barrier between the body’s internal and external environments, the skin plays an essential role in protection against mechanical, chemical, and ultraviolet damage, as well as infection by microorganisms. Variability in skin quality provides information about numerous fitness-related variables, including the environment to which an individual has been exposed, as well as how the individual has responded to that environment.

Skin texture provides information about both current and long-term nutritional state, with many nutritional deficiencies being associated with skin disorders. Malnutrition causes skin dryness, and vitamin deficiencies—whether the result of malnutrition, malabsorption, or genetic defects—are associated with skin abnormalities, including inflammation, hyperpigmentation, and impaired healing of wounds (see Piccardi & Manissier, 2009, for review).

Irregular skin texture can also cue health issues. Psoriasis, an inflammatory disease linked to immune dysregulation, is characterized by the presence of thick, scaly red plaques (Feng et al., 2009), and, in women, ovary malfunction and overproduction of androgens is linked to skin lesions (Schiavone et al., 1983). Conversely, smooth skin texture cues the ability to heal without infection (Sugiyama, 2004a).

Because skin quality is linked with age, it may also be a reliable cue to fertility and future reproductive capacity. Damage to the skin accumulates with time; fine lines, wrinkles, and unevenness in skin color increase with age (Farage et al., 2009). Consequently, smooth, homogeneous skin may reliably cue youth and residual reproductive value.

Although future research is needed to determine precisely which fitness-related information is conveyed by p. 191 distinct skin-based cues, it appears safe to assert that numerous ↳ features of the skin communicate important information about several dimensions of mate quality. We should therefore expect selection to have favored attractiveness-assessment mechanisms that track skin quality in potential mates and regulate perceptions of attractiveness in response to it.

Numerous studies support this hypothesis. Skin texture influences perceptions of attractiveness in both men and women (e.g., Fink et al., 2001), and skin smoothness and color homogeneity increase perceptions of women’s attractiveness (e.g., Fink et al., 2018). We are unaware of any studies that demonstrate effects in the opposite direction or an absence of these effects; available evidence uniformly suggests that human information-processing mechanisms attend to cues to skin quality and regulate perceptions of attractiveness in response to it.

Hair

Like skin quality, hair length and quality may reliably cue age, and therefore fertility and future reproductive capacity. With age, hair becomes thinner and dryer (Trüeb, 2009) and is more susceptible to breakage; hair strength is highest at around twenty years of age, after which it declines (Naruse & Fukita, 1971). Research has also found that hair grows fastest around the ages of peak fertility and that hair qualities such as shine, volume, and smoothness are predictive of women’s health, youth, and reproductive capacity (see Etcoff, 1999; Hinsz et al., 2001). Consistent with this, women’s hair becomes coarser and more brittle following pregnancy and with advanced age (see Symons, 1995).

Hair also conveys information about nutritional status. For example, low levels of keratin, fatty acids, protein, vitamins, and minerals in the diet are all associated with dry, brittle, and dull hair (Haneke & Baran, 2011). Additionally, deficiencies in iron and Vitamin D are linked with reduced hair growth and hair loss (see Amor et al., 2010; Karadağ et al., 2011).

Further research is needed to tease apart distinct hair-based cues and the different fitness-related information they convey, but current evidence suggests that shiny, strong (i.e., not brittle) hair may provide information about numerous fitness-relevant variables. Consequently, selection should have shaped attractiveness-assessment mechanisms to attend to hair length and quality.

There appear to be only a few empirical studies that have investigated the relationship between these features of hair and perceptions of attractiveness. Longer hair in women is associated with greater attractiveness (see Grammer et al., 2002), an effect that is independent of facial attractiveness (Bereczkei & Mesko, 2006). Hair density and fiber diameter also appear to have independent effects on perceptions of attractiveness (Fink et al., 2016). We await future tests of the relationship between these features of hair and perceptions of attractiveness, as hair appears to reliably cue multiple dimensions of important fitness-relevant information.

Teeth

Dental state cues multiple dimensions of fitness-relevant information. Misaligned teeth are associated with a reduced capacity to break down food in preparation for swallowing and digestion (Helkimo et al., 1978). Discolored teeth can cue metabolic, inherited, and traumatic factors, as well as environmental and dietary issues (Joiner, 2004), including poor nutrition (Bartlett et al., 2011). They also cue aging; textural changes associated with age result in the teeth becoming darker and yellower with time (Odioso et al., 2000). Tooth wear is also associated with age (van’t Spijker et al., 2009) as well as with poor nutrition, and tooth loss is linked to nutritional deficiencies (Kim et al., 2007).

Given the links between dental state and these fitness-relevant variables, we should expect selection to have shaped attractiveness-assessment mechanisms to track these tooth-based cues and regulate attractiveness perceptions accordingly.

Evidence supports this hypothesis but is relatively sparse. Aligned teeth are associated with perceptions of the “best smiles” (Koidou et al., 2018) and increased perceptions of attractiveness (Sena et al., 2017). Decay, yellowing, and abnormal spacing of teeth are all associated with decreased attractiveness (see Hendrie & Brewer, 2012). Cosmetic dentistry provides corroborating anecdotal evidence; the industry revolves around creating the impression of straighter and whiter, not more crooked or yellower, teeth (see Sarver, 2004).

In sum, teeth may reliably cue multiple dimensions of fitness-relevant information. However, compared to other cues with less reliably demonstrated links to fitness-related outcomes, there is a relative scarcity of research testing the relationship between perceptions of attractiveness and different aspects of individuals' dentition.

The Eyes: Sclera and Limbal Ring

When asked to describe the different "parts" of the eye, the typical person will identify the pupil, the "colored part" (iris), and the "white part" (sclera). This leaves out (1) *variability* in the color of the sclera and (2) the dark, semi-opaque boundary between the sclera and iris, known as the limbal ring—which also varies both between individuals and within individuals across time.

Sclera.

The whiteness of the sclera is a reliable cue to a multitude of fitness-related variables. Because the sclera itself is not pigmented, nonwhite coloration can reveal multiple conditions. Reddened sclera can indicate conjunctivitis, blepharitis, keratitis, iritis, and scleritis, as well as corneal abrasion, the presence of a foreign body, glaucoma, and subconjunctival hemorrhage (Cronau et al., 2010). Yellowing of the sclera may reflect jaundice, which is a cue to hepatic issues or problems with the gallbladder, pancreas, or blood (Roche & Kobos, 2004). Reddening, yellowing, and other deviations from whiteness in the sclera are also associated with senescence (Russell et al., 2014).

p. 193 Because scleral whiteness is inversely related to these fitness-relevant variables, we should expect selection to have shaped psychological mechanisms to attend to the whiteness of individuals' sclerae and regulate perceptions of attractiveness accordingly. Robust and reproduced empirical evidence from multiple independent laboratories bears out this hypothesis. Individuals with redder, yellower, or otherwise darker sclerae are perceived as less attractive (see Provine et al., 2013).

Limbal ring.

The limbal ring is a dark, semiopaque boundary between the sclera and the iris. Available evidence suggests that the limbal ring may be a cue to multiple fitness-related variables. First, it is a potential cue to youth. The deposition of fat and cholesterol on the outer edge of the cornea that occurs with older age results in a lighter limbal ling, and the limbal ring gets lighter and decreases in width with age (see Zheng & Xu, 2008). Second, the limbal ring may cue health status. Among younger individuals, corneal arcus, which results in a lighter limbal ring, may cue excessive cholesterol levels and associated health issues (see Barchiesi et al., 1991; Morris, 1992). Wilson's disease, a genetic disorder in which the liver is unable to properly process and excrete copper, is linked to impaired hepatic, neurological, renal, hematological, and endocrinological function—and it causes copper deposits in the eye that result in a lightening of the limbal ring (Das & Ray, 2006).

If the limbal ring is a reliable cue to these fitness-related outcomes, then we might expect selection to have favored psychological mechanisms to attend to the prominence of people's limbal rings and regulate perceptions of attractiveness accordingly. Available empirical evidence suggests that this may be the case (see Brown & Sacco, 2018; Peshek et al., 2011). Nonetheless, future research is needed to (1) more precisely identify the fitness-relevant variables cued by the limbal ring, (2) determine the extent to which the limbal ring cues fitness-related information that is nonoverlapping with that indexed by the sclera (e.g., both are hypothesized cues to age), (3) establish whether the limbal ring and sclera have independent effects on perceptions of attractiveness, and (4) more clearly resolve whether the effects of the limbal ring on attractiveness are sex-differentiated (e.g., Brown & Sacco, 2018)—or not (Peshek et al., 2011).

When: Variation in Standards of Attractiveness as Evidence of Context-Sensitive Design

In their paper in *Nature*, Yu and Shepard (1998) suggested that variability in standards of attractiveness across cultures is evidence that "standards of beauty are instead no more than artefacts of culture" (p. 321). This assertion is based on a fundamental misunderstanding of the universal human nature proposed by evolutionary psychologists. This universal human nature refers to species-typical *information-processing systems*, not universal behavior (Tooby & Cosmides, 1990; see also Al-Shawaf et al., 2019; Al-Shawaf & Lewis, 2017; Lewis et al., 2017a). By definition, the output of these information-processing systems is not fixed but rather is contingent on the inputs that the system processes from ↳ its environment. These inputs include not just the fitness-relevant cues observed in a potential mate, but also diverse other inputs that range from features of the local ecology to physiological indicators of the perceiver's own current condition (e.g., current immunological status). We know, from abundant psychological and nonpsychological examples in humans and nonhuman animals (and diverse nonanimal taxa, for that matter—from plants to protists), that evolved information-processing systems are designed to produce variable output, contingent on these numerous inputs from the environment (see Lewis et al., 2020). Humans' attractiveness-assessment mechanisms are no exception.

Much more work is needed in order to map the context-sensitivity of the information-processing mechanisms responsible for producing perceptions of attractiveness. Currently, the corpus of literature on such contextual effects is a hodgepodge. Some research has directed attention to a specific contextual variable (e.g., short-term vs. long-term mating). Other research has focused on a specific cue in conjunction with contextual variables that shift the fitness value of that cue. Some contextual effects have been discovered based on rigorous theorizing and a priori hypotheses. In other cases, contextual effects have first been observed and then explained. And when this has occurred, some of these post hoc explanations have been followed up with the generation of new, testable hypotheses as part of the complete process of observation-driven science. In other instances, these explanations have been left as little more than speculations.

A broader, more systematic approach is needed that follows three key steps. Researchers should (1) identify specific contextual variables that ancestrally shifted the fitness value of the cues discussed above (as well as as-yet-unidentified fitness-relevant cues), (2) generate a priori hypotheses about how attractiveness-assessment mechanisms should shift their output in response to these contexts, and (3) test for this hypothesized variation.

By and large, the literature has not been characterized by such a systematic approach. Nonetheless, researchers have made some important strides toward documenting the evolved context-sensitivity of humans' attractiveness-assessment mechanisms. Here, we provide a brief sampling of evolutionarily patterned contextual variation in perceptions of attractiveness.

Androgen-Linked Features

Androgen-linked features in men have been hypothesized to cue immunocompetence and the production of robust offspring—but also low levels of paternal investment. The trade-off between these hypothesized genetic benefits to offspring and the costs of low levels of paternal investment shifts across environments; the benefits of producing robust offspring are greater in environments characterized by environmental stressors that threaten survival. Consequently, we should expect selection to have shaped women's attractiveness-assessment mechanisms to place greater value on androgen-linked cues in men in environments characterized by higher mortality rates and communicable disease. DeBruine ↳ et al. (2010) tested this hypothesis by investigating variability in women's preferences for male facial masculinity across thirty countries. Precisely as predicted, women's preference for androgen-linked cues in men was greater in countries characterized by high levels of environmental stressors that could threaten survival.

Symmetry

Symmetry has been hypothesized to cue the ability to withstand environmental stressors, which can lead to perturbations during development. If so, then (1) individuals should exhibit higher mean levels of asymmetry in environments characterized by higher levels of environmental stressors, and (2) the fitness value of symmetry should be higher in such environments because it is a more reliable cue of individual quality. Consistent with the first proposition, Gray and Marlowe (2002) demonstrated that mean levels of asymmetry among foraging populations are higher than those observed in WEIRD populations. Little et al. (2007) investigated the second hypothesis by testing preferences for symmetry across two cultures: the United Kingdom and the foraging society of the Hadza of Tanzania, which, relative to the UK, has significantly higher mortality rates throughout the lifespan. Precisely as hypothesized, the Hadza exhibited a stronger preference for symmetry than did individuals from the UK.

Waist-to-Hip Ratio

For women's WHR, we describe research that has documented several contextual effects, including one that provides unique insight into the developmentally open design that evolved psychological mechanisms may have. Several studies have documented a preference among people from foraging societies for a female WHR that is higher than that preferred in industrialized nations (e.g., see Marlowe & Wetsman, 2001; Wetsman & Marlowe, 1999; Yu & Shepard, 1998). However, Sugiyama (2004b, 2015) noted that the stimuli employed in these studies appeared to conflate body fat and WHR, and his closer examination revealed two distinct, systematic effects of context. First, individuals from foraging societies appear to prefer mates with higher levels of body fat. This aligns with the notion that body fat stores have greater fitness value in conditions characterized by the threat of food shortages, and that selection therefore shaped human attractiveness-assessment mechanisms to place greater value on body fat stores under food-scarce conditions (e.g., Swami & Tovée, 2006; see also Sugiyama, 2004b). Even after taking these variable preferences for body fat into consideration, people from foraging populations *still* appeared to exhibit a preference for a higher WHR than people from WEIRD societies. However, when WHR values were standardized relative to local population distributions, the same finding emerged across WEIRD and non-WEIRD populations: a preference for *locally* low WHR (see Sugiyama, 2015, for discussion). This suggests that attractive-assessment mechanisms are somewhat *developmentally open* (see Hagen & Hammerstein, 2005): rather than producing an invariant preference for a fixed value ↳ of a cue, attractiveness-assessment mechanisms may instead be designed to learn about variability in that cue in the local socioecology and then produce preferences for values of that cue (in this case, low values) relative to the local distribution (Sugiyama, 2004b; 2015; see also Tovée et al., 2006). Such developmentally open design features of evolved psychological mechanisms (1) illustrate that learning and evolution are deeply interconnected and complementary—not competing—explanations (Al-Shawaf et al., 2019) and (2) represent an exciting avenue for future research.

Further Context Effects: Other Cues, Contexts, and Design Features

This brief sampling illustrates that human information-processing mechanisms respond to specific cues differently in different contexts as a function of the distinct adaptive problems posed by those contexts. This systematic, patterned variability in human standards of attractiveness across contexts is often predictable a priori on the basis of evolutionary reasoning and does not conflict with the notion of evolved, species-typical design (e.g., Al-Shawaf & Lewis, 2017).

In the future, we hope to see more systematic and theoretically driven investigations into contextual influences on perceptions of attractiveness. This should include investigating (1) context effects for all hypothesized fitness-relevant cues, (2) a wider range of contextual variables that shift the fitness values of these cues, and (3) a more diverse set of context-sensitive design features.

Investigating Context Effects for All Hypothesized Fitness-Relevant Cues

Contextual effects have not been systematically investigated for all hypothesized cues. In some cases, this may be because the cue (e.g., lumbar curvature) was only recently discovered, but in other cases (e.g., women's WHR), it is unclear why there have been so few investigations of context effects. Even a brief consideration of contextual shifts in the fitness value of women's WHR can yield new, testable predictions. As discussed above, a leading hypothesis for why the male mind tracks women's WHR is the parity hypothesis (see Lassek & Gaulin, 2006, 2019). As a woman's parity increases, her future reproductive potential decreases. To the extent that future reproductive potential is more important in long-term mating than in short-term contexts, we might expect attractiveness-assessment mechanisms to place greater value on women's WHR in long-term than short-term contexts—if the parity hypothesis is correct. An alternative hypothesis is that the male mind tracks WHR as a cue to women's probability of conception. If a woman's immediate probability of conception is more important in short-term than long-term mating contexts, we also might expect an effect of mating context—but in the opposite direction. This suggests that contextual influences not only await discovery but also may be indispensable for adjudicating between competing evolutionary hypotheses.

p. 197

Investigating a Wider Range of Contextual Variables

Researchers should also explore a more diverse set of contextual variables, as there are a number of such variables that shift the fitness value of a given cue. Significant attention has been directed to mating context-based (i.e., short-term vs. long-term) shifts, and such work has yielded empirical fruit. The influences of some other key variables have also been investigated, including resource scarcity and food deprivation; pathogen prevalence, mortality rates, life expectancy, and other indicators of environmental stressors and ecological harshness; and operational sex-ratio and other proxies for mating competition. We encourage researchers to continue to explore the influences of these contextual variables, but across the gamut of fitness-relevant cues rather than on just one cue at a time (e.g., DeBruine et al., 2010; Sugiyama, 2004b). We also encourage researchers to think broadly about ecological, social, and conditional (i.e., dependent on the perceiver's phenotype) variables that may influence the fitness value of a given cue (see Jennions & Petrie, 1997). For example, despite the productivity of research on shifts in the perception of attractiveness as a function of shifts in mating *context*, there is a comparative paucity of research investigating how individual differences in mating *strategy* may predict variability in perceptions of attractiveness. This is surprising, given that the logic for strategy-based shifts is virtually identical to that for context-based shifts. How individual differences in mating strategy interact with shifts in mating context (e.g., when long-term-oriented individuals are presented short-term mating opportunities) is even less explored.

Investigating a More Diverse Set of Context-Sensitive Design Features

Finally, the existing body of work on context effects has focused largely on just one type of context-sensitive design feature: shifts in the preferred *level* of a cue. For example, DeBruine et al. (2010) demonstrated that women from countries characterized by higher levels of threat to survival prefer greater *levels* of facial masculinity in men. This is sometimes referred to in the literature as a "stronger" preference for masculinity, but such usage conflates two distinct features of attractiveness-assessment mechanisms. Attractiveness-assessment mechanisms should adjust both (1) the preferred *level* of a trait and (2) the *strength* of that preference (i.e., how much value or weight is placed on that trait) across contexts. These are two different types of design feature. This distinction is important because, in some cases, the preferred level of a cue—but not necessarily the strength of the preference—should shift across contexts. In other cases, the opposite should be true. For example, if a higher WHR has greater fitness value in environments characterized by unpredictable food resources, then we should expect the preferred *level* of WHR to shift as a function of food reliability, but we might not necessarily expect the value placed on WHR in overall attractiveness assessments to change. Conversely, in short-term contexts, mating with an individual who exhibits cues to immediate fertility may be a more pressing adaptive problem than it is in long-term contexts. Consequently, attractiveness-assessment ↳ p. 198 mechanisms might place greater *value* on cues to fertility—but not necessarily prefer a different *level* of fertility cues—in short-term than long-term contexts.

More broadly, investigations that distinguish between the preferred *level* of a cue and the *strength* of that preference are needed. Toward this goal, researchers could profitably employ a more diverse set of tools for measuring preferences. Attractiveness ratings, as well as more advanced measures like slider scales where the participant can manipulate the cue to their preferred level, may not readily capture information about the *strength* of that preference. Other paradigms, such as budget allocation methods and forced trade-offs (e.g., Li et al., 2002; see also Lewis et al., 2011), on the other hand, may be better suited to answer questions about the strength of preference for a particular cue. Moreover, such paradigms will enable researchers to investigate not only the trade-offs associated with different levels of a single cue, but also trade-offs between multiple cues across contexts. For example, attractiveness-assessment mechanisms may trade off cues to future reproductive potential for cues to immediate fertility in short-term mating contexts but may do the opposite in long-term contexts. Attending to these kinds of trade-offs would be both theoretically and empirically valuable.

Other Cues: Different Perceptual Modalities and Different Relationship Types

In this chapter, we have focused on the perception of physical attractiveness in response to cues that are *morphological*, *visual*, and of fitness relevance to human *mating* relationships. Covering the entire landscape of cues relevant to interpersonal attraction is beyond the scope of a single chapter, but we wish to briefly discuss what a comprehensive discussion of human interpersonal attraction must include.

First, the mind evolved to attend not just to *visual* cues, but also to fitness-relevant cues detectable via other perceptual modalities, including auditory (e.g., Puts et al., 2011), olfactory (e.g., Jacob et al., 2002), tactile, and gustatory cues (see Caton et al., in press, for a discussion of human intersexual courtship via these distinct perceptual modalities). Abundant evidence also indicates that the mind evolved to attend to cues that are not directly produced or emitted by the target. For example, there is robust evidence that women's psychological mechanisms track cues to men's social and economic *status* and integrate this information with other aspects of mate value to regulate mating attraction (e.g., see Buss, 1989; Buss et al., 2020; Buss & Schmitt, 1993). In short, visual cues represent just one class of perceptual cues that influence the perception of an individual's physical attractiveness—and the perception of an individual's physical attractiveness is only one facet of the perception of an individual's overall mate value.

Moreover, mating attraction is only one portion of the broader landscape of interpersonal attraction in human relationships, of which there are diverse types—from short-term sexual liaisons to long-term committed partnerships, from temporary coalitional alliances to lifelong friendships. In cases where the fitness value of a cue varies across ↳ relationship types, we should expect human psychology to respond to that cue differently across distinct relationship types. We encourage the reader interested in interpersonal attraction in nonmating relationships to consult Sugiyama (2015) for a discussion of the broader concept of individuals' "social value" for nonmating relationships (see also Petersen et al., 2012).

Moving Forward: Greater Specification of Hypotheses and Design Features

An evolutionary approach to attractiveness is both indispensable and in need of several major improvements. Without this approach, many findings in attractiveness research would have seemed arbitrary and remained unexplained, and many *previously unknown* influences on attractiveness might have remained undiscovered. Despite these key contributions, we call for several key improvements in evolutionary research on attractiveness. These suggested improvements all derive from the overarching suggestion that hypotheses should be anchored more deeply in the *information-processing mechanisms* responsible for producing perceptions of attractiveness. A closer focus on these mechanisms and their design features will lead to a more precise specification of these hypotheses and a clearer picture of the predictions they generate. This will render the hypotheses more readily falsifiable, facilitate pitting them against competing evolutionary accounts, and, ultimately, lead to new discoveries about what humans find attractive and why.

When a hypothesis is underspecified—when it fails to identify, in advance, the expected design features of the hypothesized mechanism—it becomes difficult to test that hypothesis, let alone pit it against competing alternatives, including alternative evolutionary hypotheses. This underspecification of hypotheses can manifest itself at different stages of hypothesis generation. It can first arise when a researcher fails to specify the fitness-relevant variable supposedly linked to the cue of interest in the first place (Bovet, 2019). This is a critical first stage of hypothesis generation. If a hypothesis fails to do this, then it becomes difficult or impossible to generate predictions about how the perception of attractiveness in response to that cue should vary as a function of specific contextual variables. Bovet (2019) highlighted that the evolutionary literature on WHR is rife with such hypotheses, which are "vague theoretical explanation[s]" that present a nebulous argument about a particular cue being predictive of an individual's "mate value" based on some invocation of "health," "fertility," or some combination thereof (p. 3). Even if we temporarily accept the broad constructs of "health" and "fertility" as sufficiently specific, these are *different* fitness-relevant variables. Immediate *fertility* would appear to have greater relevance in short-term mating contexts than in long-term contexts. By contrast, a potential mate's *health* would certainly seem to be important for long-term mating decisions. The broader point is this: it is necessary for researchers to be explicit about the fitness-relevant information hypothesized to be indicated by the cue in order to generate predictions about the design of the information-processing mechanism that attends to that cue.

Clearly specifying the fitness-relevant information indicated by the cue will enable researchers to generate predictions about the design features of the mechanism, thereby rendering the hypothesis more readily testable. In particular, generating predictions about how the mechanism should respond to that cue across different contexts will enable more specific tests of the hypothesis *and* enhance researchers' ability to pit the hypothesis against alternative evolutionary accounts.

The WHR literature again illustrates this point well. Bovet's (2019) systematic review revealed that at least seventeen evolutionary explanations have been proposed for why men's attractiveness-assessment mechanisms attend to women's WHR. For each of these hypotheses, the specific fitness-relevant variable hypothesized to be cued by WHR should provide insight into the information-processing architecture of the proposed mechanism. For example, one hypothesis proposes that the male mind tracks WHR because lower levels of WHR are associated with greater openness to short-term mating. If this hypothesis is correct, we should expect men's attractiveness-assessment mechanisms to place greater value on low WHR in short-term than long-term contexts. By contrast, a different hypothesis proposes that the male mind tracks WHR because it is a cue to "maternal behavior" (Bovet, 2019, p. 12). If this hypothesis is correct, we should expect precisely the opposite context effect: men's attractiveness assessment mechanisms should place greater value on low female WHR in long-term than short-term mating contexts.

Together, these two contrasting hypotheses illustrate several points. First, they demonstrate the importance of being specific about the fitness-relevant information indicated by the cue; this specificity is essential for researchers to generate a priori predictions about the design features of the hypothesized information-processing mechanisms, including their sensitivity to contextual variables. Second, research needs to test for evidence of these design features. By testing for evidence of the *different* information-processing design features expected under competing hypotheses, researchers will be able to empirically adjudicate between alternative evolutionary explanations. Third, the existing shortcomings of the evolutionary literature on attractiveness truly do represent valuable future opportunities. Rather than simply discarding the loosely specified hypotheses that have been advanced, researchers can and should return to them in order to specify and test for the information-processing design features that they propose.

We hope that this approach—clearly articulating the fitness-relevant information hypothesized to be linked to the cue and generating specific predictions about how attractiveness-assessment mechanisms should respond to that cue across different contexts—is useful for refining existing hypotheses as well as for generating new hypotheses about humans' psychology of attractiveness. Ultimately, we hope that this leads to exciting new discoveries about what humans find attractive, when, and why.

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