

Explaining financial and prosocial biases in favor of attractive people: Interdisciplinary perspectives from economics, social psychology, and evolutionary psychology

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Abstract: Financial and prosocial biases in favor of attractive adults have been documented in the labor market, in social transactions in everyday life, and in studies involving experimental economic games. According to the taste-based discrimination model developed by economists, attractiveness-related financial and prosocial biases are the result of preferences or prejudices similar to those displayed toward members of a particular sex, racial, ethnic, or religious group. Other explanations proposed by economists and social psychologists maintain that attractiveness is a marker of personality, intelligence, trustworthiness, professional competence, or productivity. Evolutionary psychologists have argued that attractive adults are favored because they are preferred sexual partners. Evidence that stereotypes about attractive people are causally related to financial or prosocial biases toward them is weak or nonexistent. Consistent with evolutionary explanations, biases in favor of attractive women appear to be more consistent or stronger than those in favor of attractive men, and biases are more consistently reported in interactions between opposite-sex than same-sex individuals. Evolutionary explanations also account for increased prosocial behavior in situations in which attractive individuals are simply bystanders. Finally, evolutionary explanations are consistent with the psychological, physiological, and behavioral changes that occur when individuals are exposed to potential mates, which facilitate the expression of courtship behavior and increase the probability of occurrence of mating. Therefore, multiple lines of evidence suggest that mating motives play a more important role in driving financial and prosocial biases toward attractive adults than previously recognized.

Keywords: attractiveness; behavioral economics; evolutionary psychology; financial decision making; prosocial behavior; stereotypes

1. Introduction

Financial and prosocial biases in favor of physically attractive adults have been a phenomenon of considerable interest to economists, social psychologists, and evolutionary psychologists (throughout this article, all evolutionary behavioral scientists are referred to as evolutionary psychologists). Several different explanations have been proposed for this phenomenon. One influential model developed by economists (the “taste-based” discrimination model) assumes that these biases are the result of individual

preferences or prejudices, without explaining why these preferences or prejudices occur (e.g., Gneezy & List 2013; Hamermesh 2011). Other explanations proposed by economists and social psychologists assume that people are financially or prosocially biased toward attractive individuals because attractiveness is a reliable marker of psychological or behavioral characteristics (e.g., personality, intelligence, trustworthiness, professional competence, or productivity) (e.g., Hamermesh 2011; Hosoda et al. 2003; Jackson et al. 1995; Langlois et al. 2000). Finally, many

evolutionary psychologists have argued that financial or prosocial biases toward attractive adults occur because these individuals are preferred sexual partners (e.g., Farrelly et al. 2007; Iredale et al. 2008; Kenrick et al. 1993; Maner et al. 2003; Van Vugt & Iredale 2013); different evolutionary explanations have been used with regard to positive biases toward attractive infants and children (see sect. 6). This view implies that in order to understand financial and prosocial decision making, one also has to take into account sexual motives.

One common feature shared by the explanations advanced by economists, social psychologists, and evolutionary psychologists is that they assume that attractiveness-related biases in human social transactions originate from biases in behavior and decision making at the individual level. An alternative viewpoint adopted by some sociologists and cultural anthropologists is that such biases reflect common or recurring sociocultural or historical factors such as conflict between classes, male domination and oppression of women, or intrinsic characteristics of capitalistic socioeconomic systems (e.g., Berry 2007; 2012; Wolf 1992).

In this article, we aim to (1) describe financial and prosocial biases in favor of attractive individuals in the labor market, in social transactions in everyday life, and in studies involving experimental economic games; (2) examine the explanations for this phenomenon provided by economists, social psychologists, and evolutionary psychologists; (3) review and evaluate the empirical evidence in favor of or against these explanations; (4) discuss some possible psychological and physiological mechanisms underlying the expression of positive biases in favor of attractive individuals; and (5) discuss the development of attractiveness-related positive biases early in life. Although there is a large body of research on attractiveness-related

biases in social and developmental psychology, in this article we concentrate primarily on labor market studies and laboratory studies involving experimental economic games because we believe that these studies can provide the most direct documentation of financial and prosocial biases in favor of attractive individuals and the most useful evidence to understand their determinants. Labor market studies generally have large sample sizes and investigate attractiveness-related biases that have important real-life consequences: hiring decisions, career advancements, and wages. Laboratory studies involving experimental economic games provide the setting in which both independent variables (attractiveness) and dependent variables (decision making) are experimentally manipulated with a high degree of precision, and interactions between individuals take place according to highly standardized procedures. To our knowledge, there have been no systematic studies of the effects of attractiveness on decision making from a purely sociological or anthropological perspective; therefore, these perspectives are not addressed in this article. We do acknowledge, however, that financial and prosocial biases in favor of attractive people probably have multiple determinants and that sociocultural factors are likely to contribute to them.

2. Biases in favor of attractive individuals in the labor market and in social transactions in everyday life

The existence of a beauty premium in labor markets across industries, contexts, and cultures is well known and well documented (see Hamermesh 2011). Physically attractive individuals are more likely to be interviewed for jobs and hired, they are more likely to advance rapidly in their careers through frequent promotions, and they earn higher wages than unattractive individuals (see references listed subsequently).

A particularly effective research approach for documenting the advantage of attractive people in the job application and interview process involves sending curricula vitae (CVs) with photos of attractive and unattractive men and women to firms that have advertised job openings (e.g., Busetta et al. 2013; Lopez Boo et al. 2013; Ruffle & Shtudiner 2015). In one recent study using this approach, Busetta et al. (2013) sent 11,008 CVs to 1,542 job openings in Italy. They sent the same CV eight times to each job opening: In four cases, they included a photograph of the alleged applicant (as an attractive man, an unattractive man, an attractive woman, or an unattractive woman), whereas in the other four cases no photo was included. Callback rates were significantly higher for attractive women and men when compared with unattractive women and men (attractive women, 54%; unattractive women, 7%; attractive men, 47%; unattractive men, 26%) and with applicants without photos (39%). Overall, callback rates did not differ significantly for female and male applicants, indicating the absence of sex discrimination in the hiring process. However, there was a robust main effect of attractiveness, as well as a significant interaction between attractiveness and sex, because attractiveness mattered more for female applicants (54% vs. 7%) than for males (47% vs. 26%) (see Penninck [2014] for lack of effects of male attractiveness on callback rates).

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Beyond its effect on initial hiring opportunities (see also Bardack & McAndrew 1985; Cann et al. 1981; Dipboye et al. 1975; 1977; Gilmore et al. 1986; Hosoda et al. 2003; Quereshi & Kay 1986; Raza & Carpenter 1987), physical attractiveness is also known to be a significant predictor of career advancement and promotions (Chung & Leung 1988; Hosoda et al. 2003; Jackson 1983; Marlowe et al. 1996; Morrow et al. 1990; Ross & Ferris 1981). Finally, a growing number of studies have reported that attractive individuals earn higher wages than unattractive individuals (Biddle & Hamermesh 1998; Fletcher 2009; Frieze et al. 1991; Hamermesh & Biddle 1994; Hamermesh et al. 2002; Harper 2000; Johnston 2010; Roszell et al. 1989); in some cases, the difference is found for women, but not for men (French 2002; Sachsida et al. 2003; see also Udry & Eckland 1984). The beauty premium in the labor market has been quantified: Workers of above-average beauty earn approximately 10% to 15% more than workers of below-average beauty (Hamermesh 2011). The size of this beauty premium is economically significant and comparable to the race and gender gaps in earnings in the U.S. labor market (Hamermesh 2011).

Physical attractiveness is also associated with greater financial rewards, success, and recognition outside of the labor market. For example, using a door-to-door fundraising approach, Landry et al. (2006; see also Gneezy & List 2013) reported that men's charity donations were positively correlated with female solicitor attractiveness (blonde solicitors were particularly successful) (Price 2008). Similarly, online donations to marathon runners were more numerous and of larger amounts for attractive than for unattractive runners (Raihani & Smith 2015). The effect occurred regardless of sex; however, men increased the size of their donation to an attractive female runner after another man had made a large donation to this runner, whereas the same effect was not found for women who made donations to attractive male runners. Several studies have also reported that attractive restaurant waitresses receive larger tips from men, regardless of the quality of the service they provide (Guéguen 2012; Lynn 2009; Lynn & Simons 2000). Landy and Sigall (1974) had male undergraduate students read an essay, which they were led to believe had been written by female college freshmen whose photos of faces (prerated for attractiveness) were attached to the essay. Male students had more positive evaluations for the essay and the essay writer if the writer was attractive than if she was unattractive. Several experimental studies of helping behavior have reported that men are more likely to help attractive than unattractive women (Benson et al. 1976; West & Brown 1975; Wilson 1978), and experimental research on mock juror judgments has shown that it is advantageous for defendants to be physically attractive, female, and of high socioeconomic status, although these advantages are stronger for some crimes than for others (see Mazzella and Feingold [1994] for a meta-analysis of this research). Hamermesh and Parker (2005) showed that attractive professors at the University of Texas at Austin received better teaching evaluations from undergraduate students than less attractive professors. Finally, Hamermesh (2006) showed that more attractive economists were more likely to be elected officers in the annual elections of the American Economic Association between 1996 and 2004 (see also

Berggren et al. [2010] for further effects of attractiveness on electoral success).

2.1. Explanations for attractiveness-related positive biases

2.1.1. Explanations by economists. It is often argued by economists that the beauty premium in the labor market is a form of "taste-based" or "animus-based" discrimination (Becker 1957). In this view, individuals have a preference for attractive people or a prejudice against unattractive people, regardless of their productivity (Hamermesh 2011). This is similar to positive or negative biases in favor of or against members of particular groups (e.g., in relation to their sex, ethnicity, race, or religion). The taste-based discrimination model provides no explanation as to why a preference for attractive people or a prejudice against unattractive people exists; in fact, this model is descriptive rather than explanatory.

An alternative explanation taken into consideration by economists is that the differential treatment of attractive and unattractive employees in the labor market is a form of economic discrimination; namely, it reflects differences in productivity between them, which, according to human capital theory, may result from differences in education or training (e.g., Biddle & Hamermesh 1998; Cipriani & Zago 2011; Pfann et al. 2000). In this view, attractive people are preferred and rewarded more in the labor market because they are more profitable employees to the organizations that hire them. Finally, it has also been proposed that the beauty premium in the labor market may be the result of attractive workers' greater self-confidence and their greater ability to negotiate higher wages with their employers (e.g., Mobius & Rosenblat 2006).

Although attractiveness-related differences in workers' productivity or self-confidence could explain why attractive workers are more likely to be hired after being interviewed, advance in their careers more rapidly, and earn higher wages, neither differences in productivity nor differences in self-confidence can explain why attractive job applicants are more likely to be interviewed in the first place. To explain this bias, which entails the assumption that there are different expectations about attractive and unattractive individuals, economists generally refer to the stereotype-based theories advanced by social psychologists.

2.1.2. Explanations by social psychologists. The study of perceptual and behavioral biases toward attractive individuals has been a very active area of research in social psychology, with hundreds of studies on this topic being conducted in the period 1950–2000 (see Langlois et al. [2000] for a review and meta-analysis of this research). Social psychologists have shown or suggested that attractive people are often perceived as friendlier, healthier, and more intelligent, competent, generous, and trustworthy (the "beautiful is good" stereotype), whereas unattractive people are perceived as dull, introverted, and less generous or trustworthy (e.g., Adams 1977; Dion et al. 1972; Eagly et al. 1991; Feingold 1992a; Gillen 1981; Hosoda et al. 2003; Jackson et al. 1995; Langlois et al. 2000; Lewis & Bierly 1990; Webster & Driskell 1983; but see Dermer and Thiel [1975] as an example of opposite findings). According to stereotype-based theories (e.g., "social expectancy theory," "implicit personality theory," and "lack of fit model") (see Hosoda

et al. 2003; Langlois et al. 2000), when someone is exposed to an attractive or an unattractive individual, a stereotype is activated about what psychological traits and behavior can be expected from that person. In this view, activation of positive stereotypes relative to the personality or expected behavior of attractive people explains why these people are treated more favorably than unattractive people.

Stereotype-based explanations of the effects of attractiveness are sometimes linked to research showing that people often make attributions of personality traits, trustworthiness, and professional competence from individuals' faces (e.g., Rule & Ambady 2008; 2009; Stirrat & Perrett 2010; 2012; Todorov et al. 2005). However, the association between such attributions and physical attractiveness is complex, for example, because positive or negative attributions depend on the age, sex, and familiarity/resemblance of the face, as well as on particular facial characteristics (e.g., width, babyfacedness), which may or may not be associated with attractiveness. For example, in one study of attractiveness and corporate success, attractive male managers were judged to be more competent, whereas attractive female managers were judged to be less competent (Heilman & Stopeck 1985; see also Heilman & Saruwatari 1979; Morrow 1990; Verhulst et al. 2010; Zebrowitz & Rhodes 2004). Moreover, faces that resemble the self generate positive attributions and elicit greater prosocial behavior, but such faces are rated low in attractiveness for short-term mating (DeBruine et al. 2008).

Stereotype-based theories rarely address the functional significance of attractiveness-related stereotypes: In other words, they rarely attempt to explain why attractiveness-related stereotypes exist and why they are the way they are (e.g., why they involve the attribution of particular positive attributes to attractive individuals) (see Langlois et al. 2000). One notable exception is provided by Lemay et al. (2010), who argued that people have positive stereotypes about the psychological and behavioral characteristics of attractive individuals because they desire to form social bonds with them. In their view, exposure to attractive individuals induces a motivational state described as "attractiveness-based affiliation." Lemay and colleagues, however, did not address why people desire to form social bonds with attractive individuals and what is the precise nature of these bonds.

A more direct and comprehensive functional perspective is adopted by evolutionary explanations of attractiveness-related biases, most of which assume that attractive individuals receive financial and prosocial rewards because attractiveness is intrinsically valuable in the mating domain.

2.1.3. Evolutionary explanations. Across all human cultures, both men and women have a sexual preference for physically attractive as opposed to unattractive individuals. Research on marriage markets, responses to personal ads, online dating services, speed dating, and the like has confirmed that the preference for attractive individuals as romantic and/or sexual partners is ubiquitous and universal (e.g., Buss 1989; 2003; Buss & Schmitt 1993). The universal preference for physically attractive individuals as sexual partners is also documented by research on prostitution, which clearly shows that customers are willing to pay larger amounts of money to more attractive prostitutes (Hamermesh 2011).

Although what an individual finds attractive in a potential sexual partner may vary in relation to the sex, age, sexual orientation, and culture of the two individuals, beautiful individuals are universally recognized as such, and reliably discriminated from unattractive individuals, regardless of sex, age, sexual orientation, and culture (e.g., Langlois et al. 2000; Little et al. 2011; Rhodes 2006; Rhodes & Zebrowitz 2002; Rhodes et al. 2001a). Whether men or women are attracted to same-sex or opposite-sex individuals, individuals much younger or older than themselves, or individuals who conform to particular cultural ideals, there is always a preference for more beautiful versus less beautiful individuals within that particular category of potential sexual partners. A preference for attractive individuals as potential sexual partners may not in itself increase an individual's biological fitness (e.g., if it involves same-sex individuals); however, it is likely that over the course of our evolutionary history this preference was selected for because it increased the probability of reproducing with individuals who were healthier, stronger, more fertile, or better able to invest in offspring. In fact, human facial attractiveness is likely to be an indicator of overall quality, including greater genetic quality, lower exposure to stress during early development, greater resistance to diseases and parasites, and greater fertility (see Barber 1995; Buss 2003; Fink & Penton-Voak 2002; Gangestad & Scheyd 2005; Hume & Montgomerie 2001; Little et al. 2011; Rhodes 2006; Thornhill & Gangestad 1993). Hence, faces that have particular attributes such as averageness, symmetry, masculinity/femininity, and youthfulness or babyfacedness are judged as beautiful and presumably signal greater quality, whereas faces that lack these attributes (e.g., highly anomalous or asymmetrical faces) are judged to be ugly and presumably signal low quality. Although the common view is that there is a linear relationship between high/low facial attractiveness and quality, it has also been argued that only the link between facial ugliness and low quality is real, and that preferences for beautiful faces are a perceptual by-product of aversion to and avoidance of ugly faces (for this "anomalous face overgeneralization hypothesis," see Zebrowitz and Montepare [2008]). Although men place more weight than women do on the physical attractiveness of a potential mate than on high status or possession of resources, both men and women value the physical attractiveness of a potential mate very highly, particularly in the context of short-term mating (e.g., Buss 2003; Gangestad & Scheyd 2005).

There are three different evolutionary explanations for financial and prosocial biases in favor of attractive people: One is that the predisposition to exhibit prosocial behavior toward attractive mating partners is so engrained in the human mind that it generalizes also to social situations that have no bearing on mating. For example, it has been suggested that a "switch" for turning off such a response in all but sexual encounters would have involved more fitness costs than gains and therefore would not have evolved (Mulford et al. 1998). In this "evolutionary by-product" explanation, the beauty premium in the labor market is a nonfunctional by-product of a bias that is functional in another context, the context of mating and mate selection.

A different evolutionary explanation (the "functional evolutionary explanation") is that the bias in favor of attractive people reflects sexual attraction, but that this bias is

actually functional: Its function would be to maintain proximity to attractive people so as to increase the chances of having sexual interactions with them. In this view, decisions made by employers that benefit attractive individuals may be consciously or unconsciously made to increase the probability of gaining sexual access to these individuals. Given that it is not unusual for people to date or marry individuals whom they have met at work and for attractive female employees to experience male sexual harassment, it would be mistaken to assume that social interactions in the workplace, including financial transactions, have no bearing on mating.

A third evolutionary explanation—the “sexual signaling hypothesis”—is that by rewarding attractive individuals with lucrative job offers, promotions, and salary raises, employers are engaging in direct courtship behavior (as opposed to simply maintaining proximity) and attempting to make themselves appealing as potential sexual partners (see Miller 2000; Roberts 1998; Tessman 1995). Because traits related to willingness to share resources (e.g., kindness, generosity, altruism, and helpfulness) make a person more attractive as a mating partner (Barclay 2010; Brase 2006; Farrelly 2011; Moore et al. 2013; Oda et al. 2013), behaving prosocially toward attractive individuals who are potential mates can also be interpreted as courtship behavior aimed at increasing the probability of mating with these individuals.

The evolutionary by-product explanation is quite broad and can apply to virtually any interactions with attractive people, including same-sex interactions and temporally isolated interactions that are not conducive to long-term professional relationships. The other evolutionary explanations apply well to opposite-sex interactions, and particularly to all situations in which older and powerful male employers make hiring, career, or salary decisions about younger and attractive female employees. Although they may also apply to female employers and male employees, they are less likely to apply to same-sex interactions, unless same-sex sexual attraction is involved. In fact, the mating-related evolutionary explanations predict that heterosexual people will have negative biases against attractive same-sex individuals because these are perceived as potential sexual competitors (e.g., Agthe et al. 2010; 2011; 2014; Kenrick et al. 1993; Maner et al. 2003; 2007b; 2009b). The sexual signaling hypothesis predicts that financial generosity or prosocial behavior can be used as courtship display toward attractive potential mates not only when these individuals are the beneficiaries of these actions, but also when they witness, as bystanders, these actions being directed toward other individuals.

3. Studies addressing the possible determinants of financial and prosocial biases in favor of attractive individuals

3.1. Field studies

The hypothesis that the beauty premium in the labor market is because of differences in productivity between attractive and unattractive workers was addressed in a study of Dutch advertising firms, in which firm revenues were analyzed in relation to the physical attractiveness of company executives (Pfann et al. 2000). The authors of this study reported that the physical attractiveness of board members was associated with higher revenues in large firms, but with lower revenues in small firms. The mechanism underlying the correlations between

attractiveness and company revenues remained unclear. In an unpublished study of an online lending market in which photographs of borrowers were available as part of an application process, Ravina (under review) reported that physically attractive borrowers received better terms from lenders. Contrary to the economic discrimination hypothesis, the author also found that attractive borrowers were more likely to become delinquent on loans; therefore, they were less reliable and less profitable customers. The economic discrimination explanation was also addressed in an unpublished British study of a Dutch television game (cited by Hamermesh 2011). In this game, five players had to answer questions posed by the moderator in multiple consecutive rounds; right answers would bring monetary winnings to the players' group. At each round, the players had an opportunity to exclude from the game one of their fellow contestants. The British researchers examined whether decisions to eliminate players were accounted for by their physical attractiveness or by their ability to answer previous questions and, therefore, their ability to earn money for the group. At each round, the physical attractiveness of the player being eliminated was always lower than the average attractiveness of the remaining players. Therefore, attractiveness in itself was rewarded, whereas the productivity of the players did not matter (and there was no association between attractiveness and ability to answer questions and earn money). Finally, the hypothesis that the beauty premium results from employee productivity was specifically tested in a study by Mobius and Rosenblat (2006). The authors of this study created an experimental labor market made up of college students, in which “employers” determined wages of “workers” who performed a maze-solving task. This task required a true skill that was unaffected by physical attractiveness. Employers were tested in different conditions: baseline, in which they only reviewed workers' resumes without any information on their characteristics; visual, in which the employers saw the resume and a photo of the worker; oral, in which the employers saw the resume and had a 5-minute phone interview with the worker; visual+oral, in which the employers saw the resume and the photo and had a 5-minute phone interview with the worker; and face-to-face, in which the employers saw the resume and the photo and had a 5-minute face-to-face interview with the worker. There was no beauty premium in the baseline condition, but attractive workers were offered higher wages in all of the other conditions, the highest (17%) being in the face-to-face condition.

Mobius and Rosenblat (2006) proposed that the beauty premium in their experimental labor market may have been the result of the attractive workers' greater self-confidence and greater ability to negotiate higher wages with employers when they interacted face-to-face with them. However, the study showed that even when self-confidence was controlled for, attractive employees received higher wages. In a Canadian study of the labor market (cited by Hamermesh 2011), physical attractiveness and self-confidence were positively correlated, but the correlation was weak. Again, even when their self-confidence was controlled for, attractive individuals earned higher wages. Finally, Leigh and Borland (2007) analyzed the relationship between attractiveness and labor market outcomes using an Australian database known as the 1984 National Social Science Survey. This database contains information on

earnings, attractiveness of respondents rated by interviewers, and self-rated attractiveness by respondents. Regressions were run in which the dependent variable was a labor market outcome (employment or hourly wages) and independent variables were the respondent's interviewer-rated beauty and self-perception of beauty. Objectively assessed beauty was associated with higher wages, but self-perceived beauty was not. The authors concluded that the beauty premium was because of others' responses to physical appearance, whereas self-perceived attractiveness (and presumably also self-confidence) did not matter.

3.2. Studies involving experimental economic games

3.2.1. Experimental economic games. Controlled laboratory experiments to investigate biases in behavior and decision making are used by many behavioral scientists who believe that the behavior observed in these settings is representative of human behavior in general and related to economic processes at the societal level. To this end, experimental paradigms have been designed – referred to as experimental economic games – that are informed by theoretical models of behavior and are highly standardized in terms of procedures and data collection and interpretation. The experimental economic games that have been most commonly used in behavioral research include the prisoner's dilemma, the trust game, the ultimatum game, the dictator game, and the public goods game (see Camerer 2003). Each of these games sheds light on different aspects of decision making in the context of social transactions between two or more individuals. When economists study decision making in experimental economic games, they often conceal information about the players' identities and their characteristics, so as to minimize the influence of these “confounding” variables. One can take the opposite approach, however, and use economic games to investigate precisely how players' identities and characteristics, as well as the circumstances of their interactions, influence decision making and behavior in the real world (e.g., Andreoni & Petrie 2008; Eckel 2007; Hancock & DeBruine 2003). For example, behavioral economists such as Andreoni and Petrie (2008) have argued that studying the effects of sex and attractiveness on decision making in economic games can elucidate why these factors play an important role in the labor market.

3.2.2. Effects of physical attractiveness on behavior in economic games. Evidence for effects of physical attractiveness on decision making in a laboratory setting has been provided by numerous studies involving the prisoner's dilemma, the dictator game, the ultimatum game, the trust game, and the public goods game. These effects are all in the same direction (i.e., attractive individuals are treated more favorably) and are generally consistent regardless of how attractiveness is assessed, for example, through subjective self-ratings, third-party ratings, or using physical characteristics that are generally associated with physical attractiveness such as facial symmetry, waist-to-hip ratio (WHR) for women, facial femininity for women and masculinity for men, and body mass index (BMI). Although many studies report a main effect of attractiveness such that attractive men and women receive more favorable treatments, interactions between the sex and attractiveness of the two players have also been reported. In addition to investigating the occurrence and magnitude of the effects

of attractiveness on decision making, many studies involving economic games have also made attempts to understand the mechanisms underlying these effects.

In one of the earliest studies examining the effects of sex and attractiveness on decision making in economic games, Kahn et al. (1971) had male and female participants play a yoked prisoner's dilemma game with opposite-sex partners. Participants were randomly assigned to one of two different conditions, one in which the optimal response was to cooperate and the other in which it was to compete with the other player. Participants were more likely to cooperate with attractive than with unattractive partners, although the effect of partner attractiveness was partially modulated by the player's sex, the player's own attractiveness, and the experimental condition (i.e., whether it was optimal to cooperate or to compete). In particular, men always cooperated more with attractive female players, regardless of their own attractiveness and whether cooperation or competition was optimal. Women cooperated more with attractive men when cooperation was optimal but not when it was not optimal, and the effect of partner's attractiveness was stronger for unattractive than for attractive women. This study thus provided early evidence that both men and women are biased in favor of attractive opposite-sex partners and that these biases are expressed more consistently by men than by women.

In a more recent study with similar experimental procedures, participants could choose with whom they wanted to play a prisoner's dilemma game (Mulford et al. 1998). After playing the game, participants assessed both their own and their partner's physical attractiveness (attractiveness was also independently rated by observers). Participants also provided an assessment of their expectation that players would cooperate in the game. The authors found that participants were both more likely to enter a game and more likely to cooperate with others they found more physically attractive. As in the study of Kahn et al. (1971), tendencies to cooperate with attractive versus unattractive players were modulated by sex and one's own attractiveness (e.g., attractive women were generally less likely than unattractive women to cooperate with both sexes, whereas the opposite was true for attractive men; furthermore, the preference for attractive players was greater for attractive than for unattractive men and women). The results obtained with choices to enter the game and to cooperate versus defect were similar. Therefore, attractive players were given more opportunities to engage in social exchange, and they received more cooperation. Although participants expected more cooperation from players whom they rated as highly attractive, the tendency to prefer attractive players was independent of this expectation of behavior. Hence, although this study confirmed the existence of a stereotype about the cooperative tendencies of attractive people, it also showed that the tendency to prefer attractive players was independent of this stereotype.

Further evidence for biases in favor of attractive individuals has been provided by studies using the ultimatum and the dictator game. Solnick and Schweitzer (1999) conducted a study in which participants played an ultimatum game, then they were photographed, and these photos were rated for attractiveness by a panel of judges. The most and the least attractive photos were then used in another ultimatum game in which subjects viewed these photos and made ultimatum game decisions that were resolved by pairing

their decisions with those of the photographed subjects. Attractive and unattractive men and women in the photos made similar offers and demands (i.e., specified similar minimum acceptable levels). However, attractive people were offered more money, regardless of their sex. They did not demand more; they were offered more because they were attractive. No explanations for this effect were provided, and possible differences between same-sex and opposite-sex interactions were not investigated. Rosenblat (2008) conducted a study with a dictator game, in which allocators listened to a speech recorded by recipients and were also shown their photos before making their decision. Allocators (females more than males) gave more to physically attractive male and female recipients (there was no significant difference in relation to sex of the recipient). In a similar study conducted by Zaatari et al. (2009), male and female participants made offers in an ultimatum game to symmetrical and asymmetrical faces of opposite-sex individuals. Subjects made higher offers to photos they rated as attractive, and more symmetrical faces were rated as more attractive than less symmetrical faces.

The hypothesis that decision making in economic games may be influenced by attractiveness-related mating motives was explicitly addressed by a study conducted by Farrelly et al. (2007), in which they tested the following predictions. First, heterosexual participants should be more cooperative with individuals of the opposite sex. Second, participants should be more cooperative when opposite-sex partners are more attractive. Third, males should show a stronger cooperative bias than females when paired with attractive players of the opposite sex. Fourth, more cooperative partners should be judged to be more attractive. Subjects played four games (a mutualism game, a prisoner's dilemma, a standard dictator game, and a charity dictator game) with four virtual players (four attractive or unattractive males and females). They were told that they were interacting with real people via the Internet (in reality, their opponents were virtual players) and that they would be able to meet the players in person in the future. Participants were randomly allocated to one of two conditions: cooperative or uncooperative partners (the responses of the virtual players were pre-programmed). The first prediction, that participants should be more cooperative with opposite sex partners, received mixed support. The prediction that participants should be more cooperative toward more attractive members of the opposite sex received support in both sexes in all games. Cooperation was not influenced by the attractiveness of same-sex partners in any game. The prediction that males, more than females, would favor more attractive members of the opposite sex was not supported. Finally, more generous partners were rated as more attractive in every case.

Some of the findings by Farrelly et al. (2007) were replicated and extended by a study by Lucas and Koff (2013), who had female participants play ultimatum and dictator games using photographs of other male and female players that had been rated for attractiveness. The authors of this study found a significant sex of partner \times attractiveness interaction predicting the amounts offered in both the ultimatum game and the dictator game. In the ultimatum game, female participants offered higher amounts to attractive men but not to attractive women. In the dictator game, both attractive men and attractive women received higher offers, but the effect of attractiveness was stronger for men than for women. This study also showed that women were more

favorably biased toward attractive men when they were fertile than when they were not fertile.

Effects of attractiveness have also been reported in trust games and in public goods games. In a study by Wilson and Eckel (2006), male and female subjects had their photos rated for attractiveness by independent judges and then played trust games, in which they sent varying amounts of money to other players, after viewing their photographs, under the expectation that this money would be later reciprocated. Attractive partners were trusted more (i.e., they received more money) than unattractive ones. Trustees were also asked to guess how much money was going to be sent. They expected higher amounts of money from attractive trusters. If these expectations were not met, attractive trusters were punished by imposing a penalty. Data were not analyzed in relation to the sex of truster and trustee. The authors argued that their results were consistent with stereotype-based explanations but provided no evidence that expectations about the behavior of attractive individuals were causally related to greater trust in these individuals. Stirrat and Perrett (2010) found that facial attractiveness in photos positively correlated with perceived trustworthiness, but attractiveness and trustworthiness had separate and independent effects on decision making in a trust game (see also Van't Wout and Sanfey [2008] for similar results).

Andreoni and Petrie (2008) conducted a study with public goods games in which they showed each player digital photos of all other members of their group. In one condition, total group contributions were known but individual contributions were kept anonymous, whereas in the other condition each player's contribution was revealed. The results showed that in the condition in which individual contributions were anonymous, participants who were rated as highly attractive made approximately 12% more than participants who were rated as unattractive. The attractiveness effect was stronger for women than for men. In the second condition, however, the difference was reversed so that unattractive people made approximately 8% more than attractive people. The explanation for the results obtained in the second condition, when contributions were not anonymous, was straightforward and related to differences in behavior between attractive and unattractive people. In this condition, attractive players made fewer contributions to the public good and therefore were punished by unattractive people, who reduced their cooperation. In the anonymous condition, however, there were no differences in contributions to the public good between attractive and unattractive people. Instead, attractive people spontaneously engendered more cooperation from other players, suggesting that in the absence of any information about contributions, there is a clear bias in favor of attractive people, particularly women.

In a study by Li and Zhou (2014), participants observed a dictator game in which proposers made offers to anonymous recipients. The participants, acting as the interest-free third party, evaluated the reasonableness of the offers and made decisions as to whether to punish the proposers. The design of the study included conditions in which male and female participants observed attractive or unattractive proposers of the same or the opposite sex. There was a main effect of offer fairness (unfair offers were punished more than fair ones) and a main effect of proposer attractiveness (attractive proposers were punished less than unattractive ones), as well as interactions

between participant's sex, proposer's sex, and proposer's attractiveness. The beauty premium, in terms of reduced probability of being punished, was strongest for opposite-sex individuals: Attractive opposite-sex proposers were punished less by participants than attractive same-sex proposers; moreover, male participants were particularly lenient of attractive female proposers.

3.2.3. The effects of attractive bystanders on behavior in economic games. The association between attractiveness and positive financial and prosocial biases has been reported not only in studies in which attractive individuals are active participants in experimental economic games, but also in studies in which they act as bystanders—in other words, when a game between two players is observed by an attractive third-party individual who does not participate. In one of these studies, conducted by Iredale et al. (2008), male and female participants played social dilemma games and made charity donations under three different audience conditions. One group of participants made decisions under anonymity conditions, a second group made decisions with a physically attractive same-sex observer, and a third group made decisions with a physically attractive opposite-sex observer. Results showed that male charity donations were significantly higher in the mixed-sex observer condition compared with the same-sex observer condition and the anonymity condition. However, female charity donations did not vary across conditions. Van Vugt and Iredale (2013) further explored the effects of attractive third-party observers on decisions made in a one-shot public goods game. In this study, a confederate sat near the computer and watched as participants made contributions to the public good. Men being observed by an attractive woman made larger contributions to the public pool, as compared with men with an attractive male observer and men with no observer. In a second experiment, Van Vugt and Iredale (2013) also found that men with an attractive female observer made larger contributions to the public pool in a repeated public goods game and that they volunteered to spend more hours doing charitable work in their spare time, as compared with men with an attractive male observer and men with no observer. Finally, Jensen (2013) extended the design of Van Vugt and Iredale (2013) by manipulating the attractiveness of the observer, such that both attractive and unattractive observers of the opposite sex were included in the study. Specifically, men played the dictator game, the trust game, and the public goods game in two conditions: while being observed by an attractive woman and while being observed by an unattractive woman (in contrast, the men in the studies by Van Vugt and Iredale were being observed by attractive women or attractive men). There was a significant effect of women's attractiveness on men's behavior, as predicted, but it was moderated by men's assertiveness (i.e., dominance). The effect was strong in nondominant men but weak in dominant men.

4. Evaluating the evidence

4.1. Evidence in favor or against different explanations

The taste-based discrimination model acknowledges the existence of preferences for attractive individuals but does not address the origin or functional significance of

such preferences. The study of earnings in Dutch firms by Pfann et al. (2000) provided partial support for the hypothesis that attractive workers are more productive. However, the hypothesis that the beauty premium in the labor market is accounted for by the greater productivity of attractive workers was contradicted by the study of online lenders and borrowers by Ravina (under review), by the British study of the Dutch television show (cited by Hamermesh 2011), and more importantly by the study by Mobius and Rosenblat (2006) in which workers' skills and productivity were clearly unrelated to their attractiveness.

Mobius and Rosenblat's suggestion that the beauty premium may be accounted for by attractive employees' self-confidence was contradicted by their own results (the beauty premium persisted after workers' self-confidence was controlled for), by a Canadian study of the labor market (cited by Hamermesh 2011) showing that attractive individuals earned higher wages even when their self-confidence was controlled for, and by the study by Leigh and Borland (2007) in which the beauty premium was unrelated to self-perceived beauty. Taken together, the findings of these studies provide little evidence for a correlation between workers' attractiveness and their productivity or self-confidence (see also the meta-analysis of attractiveness research in social psychology conducted by Langlois et al. [2000], which showed that differences in self-perceptions and competence between attractive and unattractive individuals are small). Moreover, there is little or no evidence that differences in productivity or self-confidence between attractive and unattractive workers are causally related to positive biases in favor of attractive workers (see also Hamermesh 2011; and Langlois et al. [2000], who reached a similar conclusion for attractiveness biases outside of the workplace).

Because empirical support for economists' explanations for the effects of attractiveness is weak, economists have sometimes avoided any explanations for this phenomenon altogether (e.g., Gneezy & List 2013) or have invoked the explanations proposed by social psychologists, according to whom favorable biases toward attractive people are the result of expectations about the personality traits and the interpersonal behavior of attractive and unattractive people (e.g., Andreoni & Petrie 2008). Although stereotype-based explanations are plausible, the association between perceived positive traits and attractiveness is not as robust as the beauty premium effect in the labor market (e.g., Segal-Caspi et al. 2012). Furthermore, studies of the labor market that had information about personality traits found that attractive employees earned higher wages even after controlling for personality traits (e.g., Fletcher 2009; Harper 2000; see also Baert & Decuyper 2014), leading Hamermesh (2011) to conclude that the impact of beauty on earnings appears to be independent of any association between beauty and personality. Evidence from experimental studies is equally weak. For example, in the study by Mobius and Rosenblat (2006), physically attractive workers were expected to perform better by employers, despite the fact that differences in skills among workers were unrelated to their attractiveness. The authors interpreted this finding as being consistent with stereotype-based theories. Their study, however, provided no evidence that the employers' expectation about the performance of attractive workers played a causal role in their willingness to pay them higher wages. A

meta-analysis of the effects of attractiveness on hiring decisions reported that biases in favor of attractive people are independent of the amount of job-relevant information employers have about their potential employees (Hosoda et al. 2003). This argues against stereotype-based hypotheses, which predict that the effects of attractiveness on hiring decisions should be stronger when little information is available about potential employees and weaker when more information is available (Hosoda et al. 2003). Similarly, in their meta-analysis of attractiveness research in social psychology, Langlois et al. (2000) showed that the association between attractiveness and preferential treatment is independent of familiarity: The effects of attractiveness are as strong when agents and targets know each other as when they do not (e.g., in ongoing romantic relationships, people report more passionate love, intimacy, and commitment when their partners are physically attractive; Sangrador & Yela 2000).

Similar to the study by Mobius and Rosenblat (2006), in some experimental studies with economic games in which participants were asked to estimate the future cooperation of attractive players, the existence of a positive stereotype was confirmed (e.g., Mulford et al. 1998; Wilson & Eckel 2006; but see Muñoz-Reyes et al. [2014], in which participants had a right expectation about the uncooperative behavior of attractive players). No study, however, has provided evidence that the attractiveness stereotype is causally related to the preferential treatment of attractive people (see also Langlois et al. [2000], who concluded that stereotype-based theories are largely unproven explanations of the attractiveness effects). In fact, in some studies, the effects of attractiveness were found after controlling for stereotypes and, therefore, independent from them (e.g., Mulford et al. 1998).

Direct experimental evidence that positive stereotypes do not cause prosocial biases toward attractive individuals was provided by the study by Lemay et al. (2010). Lemay and colleagues hypothesized that perception of attractiveness leads to enhanced motivation to affiliate with the attractive target, and this in turn leads to the attribution of positive characteristics to the attractive target. In other words, as a result of their motivation to form close bonds with attractive individuals, people construct images of attractive individuals as interpersonally receptive and responsive in return. Lemay et al. showed that people attributed more desirable interpersonal traits (e.g., extraverted, generous, kind, and warm) to physically attractive strangers portrayed in photos relative to unattractive strangers. This effect was explained by the subjects' desire to establish relationships with the attractive strangers (data were not analyzed in relation to the sex of the perceiver and of the target). The alternative mediation model (derived from traditional stereotype theories), according to which perception of attractiveness leads to attribution of positive traits, which in turn leads to affiliative motivation, was not supported by the data. These results were replicated in two additional experimental studies involving, instead of strangers, attractive and unattractive romantic partners or friends. Lemay et al. concluded that the beautiful-is-good effect is explained by a combination of attractiveness-based motivation to bond and projection of that motivation to attractive individuals. Therefore, the motivation to behave prosocially toward attractive individuals pre-exists the attribution of positive characteristics to

them and is not caused by them, as assumed by stereotype-based theories. The most striking finding of the study by Lemay et al. was that once the subjects' motivation to affiliate with the attractive targets was controlled for, the attractive targets were perceived in more negative, but perhaps more realistic, terms.

Similar results had been provided by an earlier study by Snyder et al. (1977), in which male college students were shown photos of attractive and unattractive female students and told that they would be able to talk with them on the phone later. Men who anticipated talking with physically attractive partners expected to interact with sociable, poised, humorous, and socially adept women; whereas men anticipating unattractive partners fashioned images of unsociable, awkward, serious, and socially inept women. However, as in the study by Lemay et al. (2010), men's attribution of positive characteristics to the attractive females was likely an inconsequential by-product of their motivation to sexually flirt with them, which they did during the course of later "getting to know each other" phone conversations (although the women in these conversations were not those shown in the photos). The study provided no evidence for a causal role of stereotypes in the positive biases toward attractive opposite-sex individuals, whereas the men's sexual flirting behavior suggested that mating motivation was important.

Studies with experimental economic games have reported that the positive stereotypes about the prosocial behavior of attractive individuals (e.g., their friendliness or generosity) simply do not correspond to reality (see also Feingold [1992] and Langlois et al. [2000] for lack of an association between attractiveness and intelligence; Jackson et al. [1995] for lack of an association between attractiveness and competence; and Segal-Caspi et al. [2012] for lack of an association between attractiveness and positive personality traits in women). Although a few studies found no significant differences in behavior between attractive and unattractive people in experimental economic games (for the ultimatum game: men or women, see Solnick & Schweitzer [1999]; for the ultimatum game: women, Takahashi et al. [2006]), there is little evidence that attractive people are more cooperative/generous/trustworthy (only one study reported this and only in men: Mulford et al. [1998]), whereas the overwhelming majority of studies have reported that attractive people, both men and women, are less cooperative, less generous, less trusting, and less trustworthy (men: Andreoni & Petrie 2008; Eckel 2007; Sanchez-Pages & Turiegano 2010; Shinada & Yamagishi 2014; Takahashi et al. 2006; Zaatari & Trivers 2007; women: Andreoni & Petrie 2008; Eckel 2007; Mulford et al. 1998; Muñoz-Reyes et al. 2014; Zaatari & Trivers 2007).

The most likely explanation for these findings is that attractive people expect favorable treatment from others because of their physical appearance (for evidence of this, see Smith et al. [2009]) and therefore are less inclined to cooperate and more likely to exploit others. This explanation is generally consistent with the evolutionary explanations for the effects of attractiveness on decision making: In these explanations, attractiveness has intrinsic value (because attractive individuals have high mate value) rather than simply being a marker of personality or behavior. Given that attractiveness has intrinsic value, people's willingness to invest prosocially and financially in attractive

individuals can be explained by the possibility that such investment may be reciprocated in a different currency. Transactions in which physical attractiveness is traded for financial and other resources are well known in human mating and marriage markets, in which young and physically attractive women are often paired with wealthy and powerful men (e.g., Buss 2003). Further evidence in favor of evolutionary explanations comes from the finding that financial and prosocial biases in favor of attractive individuals are moderated by sex.

4.2. Effects of sex on financial and prosocial biases in favor of attractive individuals

In their meta-analysis of attractiveness research in social psychology, Langlois et al. (2000) did not find significant sex differences in the importance of attractiveness. This meta-analysis, however, did not include labor market analyses or laboratory studies with experimental economic games. Moreover, Langlois et al. (2000) acknowledged that much research included in their meta-analysis examined only a single sex as target or did not distinguish between males and females (as actors) in the data analysis. If the effects of opposite-sex attraction and same-sex competition are not analyzed separately, these effects can potentially cancel each other out, resulting in no sex differences in attractiveness biases.

Table 1 presents a summary of studies in which financial and prosocial biases in favor of attractive individuals were analyzed in relation to the sex of the target (i.e., the individual receiving favorable treatment) and the relative sex of the two individuals in the interaction (i.e., interactions in which attractive individuals received favorable treatments, and such treatments were provided either by an individual of the same sex or by one of the opposite sex). Also included are two bystander studies, one of which examined participants' charity donations in the presence of an attractive bystander of the same sex, of the opposite sex, or without an audience (Iredale et al. 2008). Among studies that analyzed the effects of target sex ($n = 14$), attractiveness-related biases were reported more often (or were stronger) for female targets ($n = 9$) than for male targets ($n = 1$; this is a study in which effects were significant for both sexes but stronger for men; no study has reported significant effects for men but not for women; four studies reported no significant effects of target sex). Among studies that examined financial and prosocial biases in same-sex versus opposite-sex interactions ($n = 8$, including a study with two different experiments), such biases were reported most often (or found to be stronger) in opposite-sex interactions ($n = 7$). One study reported no significant differences between same-sex versus opposite-sex interactions. In no cases were significant financial or prosocial biases toward attractive people only found (or found to be stronger) in same-sex interactions.

The information summarized in Table 1 is relevant for assessing the different models or explanations advanced to describe or account for financial and prosocial biases in favor of attractive people.

The information presented in Table 1 suggests that the taste-based discrimination model, which assumes that people have a generic preference for beauty, does not provide an accurate description of attractiveness-related biases in financial and prosocial decision making. People

express a taste for beauty only in some circumstances, in relation to their own sex and the sex of the individual with whom they are interacting.

The effects of sex reported in Table 1 are not predicted by any hypotheses that assume that physical attractiveness is a marker of psychological traits or behavior. They are predicted, however, by evolutionary theories of attractiveness biases, according to which attractive individuals of the opposite sex are viewed as desirable potential mates, whereas attractive individuals of the same sex are viewed as sexual competitors (e.g., Maner et al. 2007; 2009). The biases in favor of attractive, lower-level female employees in the labor market are presumably linked to the overrepresentation of men in positions of power, including positions in which hiring, promotion, and salary decisions are made (e.g., Cash & Kilcullen 1985; French 2002). In fact, studies have shown that when employers are women, attractive female job candidates are less likely to be hired than unattractive ones, a phenomenon that is usually explained in terms of jealousy and envy related to same-sex competition (Agthe et al. 2010; 2011; 2014; Luxen & Van de Vijver 2006; Ruffle & Shtudiner 2015); some evidence for this also exists for men, as reported by Agthe et al. (2010; 2011). This is consistent with the results of a study involving ultimatum and dictator games, which showed that women in the fertile phase of their menstrual cycle were less generous toward attractive women when compared with unattractive women (Lucas & Koff 2013).

If stereotype-based theories were right, and if the attractiveness of potential employees simply signaled their friendliness, trustworthiness, competence, or productivity, why would male employers be more sensitive to women who have these qualities than to men, other things being equal? In fact, there is no evidence that attractive women are more competent or more productive employees than attractive men. Moreover, meta-analyses of studies of attractiveness-related stereotypes found that these stereotypes are not affected by the sex of target or sex of judge (Eagly et al. 1991; Feingold 1992a; Langlois et al. 2000; see also Webster & Driskell 1983). Another recent meta-analysis of sex differences in cooperation in social dilemmas concluded that men and women do not differ in their overall amounts of cooperation (Balliet et al. 2011; see also Croson & Gneezy 2009), although there is some conflicting evidence for sex differences in cooperation with same-sex versus opposite-sex partners (Balliet et al. 2011; Saad & Gill 2001).

The finding that the effects of attractiveness on financial and prosocial decision making are moderated by the sex of the target and the relative sex of the interacting individuals is predicted by the functional evolutionary and sexual signaling hypotheses. Both hypotheses predict that financial and prosocial biases in favor of attractive individuals should be limited to or be stronger in opposite-sex versus same-sex interactions (for heterosexuals; the opposite should be true for homosexuals). Although both men and women are expected to manifest positive biases toward attractive potential mating partners, men probably have more opportunities to express these biases, and men's biases are less likely to be constrained by sociocultural factors than women's biases.

The finding reported by some studies (e.g., Mulford et al. 1998) that attractive heterosexual individuals express a stronger bias in favor of attractive individuals of the opposite sex (but see Kahn et al. [1971], who reported a stronger effect

Table 1. (Maestripieri et al.). Summary of studies reporting whether the financial or prosocial biases in favor of attractive individuals were reported only for men (OM), stronger for men (SM), stronger for women (SW), only for women (OW), or not different in relation to sex (ND); and whether these biases were reported only in opposite-sex (OOS) interactions, stronger in opposite-sex (SOS) interactions, stronger in same-sex (SSS) interactions, only in same-sex (OSS) interactions, or not different in relation to the relative sex of the interacting individuals (ND).

Reference	Sex of Recipient (M, W)					Relative Sex of Interactants (SS, OS)				
	OM	SM	ND	SW	OW	OOS	SOS	ND	SSS	OSS
Andreoni and Petrie (2008)				X						
Busetta et al. (2013)				X						
Farrelly et al. (2007)			X			X				
French (2002)					X					
Guéguen (2012)						X				
Hamermesh (2006)		X								
Iredale et al. (2008)*					X	X				
Kahn et al. (1971)				X						
Landry et al. (2006)					X					
Li and Zhou (2014)				X					X	
Lucas and Koff (2013)**						X	X			
Penninck (2014)					X					
Raihani and Smith (2015)			X							
Rosenblat (2008)			X					X		
Sachsida et al. (2003)					X					
Solnick and Schweitzer (1999)			X							
Van Vugt and Iredale (2013)*						X				

*Bystanders.

**The study involved two different games.

for unattractive than for attractive women and no difference for men) is predicted by the evolutionary explanations considered in this article but not by any of the other models we have discussed. Attractive individuals have high mate value and therefore are more likely to select potential mating partners of equally high value than unattractive individuals (Buss 2003). The effect of one's own attractiveness on the tendency to express financial and prosocial biases toward attractive individuals, however, has been taken into consideration only in a few studies, and no firm conclusions concerning this variable can be drawn (but see the effects of one's own attractiveness on biases about others in Agthe et al. [2010] and Lee et al. [2008]). The finding that women are more biased in favor of attractive men during fertile than during nonfertile phases of their menstrual cycle (Lucas & Koff 2013) is also consistent with the evolutionary explanations and not predicted by any of the other models, but this finding needs to be replicated by other studies before any conclusions about female fertility can be made.

Further evidence consistent with evolutionary explanations comes from studies involving experimental economic games in which attractive individuals are bystanders. Stereotype-based theories predict that the attractiveness of a third-party observer should not matter because this individual is not involved in the game, and therefore, expectations of his/her future behavior based on attribution of personality traits or behavioral tendencies are simply irrelevant. In contrast, the sexual signaling hypothesis predicts that individuals should be more cooperative not only when playing with an attractive player, but also when a dyadic game is observed by an attractive third-party individual. Accordingly, studies have reported that men express greater prosocial behavior in economic games played in the presence of an attractive female bystander. Consistent with these results, other studies have shown that when being observed by a woman, men engage in more helping of strangers in need (Latané 1970), are more generous toward panhandlers (Latané 1970; but see Goldberg [1995], who found that men accompanied by their partner are less likely to donate to female panhandlers), and are more motivated to make physical sacrifices for the group (McAndrew & Perilloux 2012) or more willing to donate money to others (Tognetti et al. 2012).

Overall, the results of studies with experimental economic games, in which decision making is examined under controlled laboratory conditions and in which financial and prosocial biases in favor of attractive individuals are objectively quantified, provide the strongest support for evolutionary explanations. Studies investigating the psychological and physiological mechanisms by which mating motives in human social interactions affect behavior and decision making provide a more comprehensive understanding of the evolutionary bases of financial and prosocial biases in favor of attractive people.

5. Psychological and physiological mechanisms underlying positive biases toward attractive individuals

5.1. Emotional and neural responses to visual exposure to attractive faces

It has long been known or suspected that exposure to physically attractive individuals is rewarding and generates

positive emotions (e.g., Byrne et al. 1968). A more recent study showed that subliminal presentations of attractive faces prime positive emotion concepts (Olson & Marshuetz 2005), suggesting that positive affective reactions to attractive faces may be automatic. However, although exposure to an attractive opposite-sex individual leads to positive affect, exposure to an attractive same-sex individual may lead to negative affect (e.g., lower mood; Kenrick et al. 1993). In a study by Hazlett and Hoehn-Saric (2000), women viewed slides of adult male and female faces that varied in attractiveness. When women viewed male faces, ratings of felt pleasure, arousal, and to a lesser extent zygomatic muscle activity (measured with facial electromyography, or EMG) were greater in response to the attractive males than to the unattractive males. When women viewed female faces, the highly attractive targets evoked greater mean corrugator muscle (brow lowering muscle) EMG and greater reported arousal, whereas reported pleasure was not affected by target attractiveness. The authors' interpretation of these results was that women viewed attractive men as potential mating partners and attractive women as potential sexual competitors.

Studies in which neural activation was measured in response to exposure to same-sex and opposite-sex attractive and unattractive faces have provided further evidence consistent with the evolutionary explanations of the effects of attractiveness in terms of mating motivation. In a study by Aharon et al. (2001), young heterosexual males rated pictures of beautiful males and females as attractive but exerted effort via a key-press procedure only to view pictures of attractive females. Therefore, although ratings of beauty for same-sex and opposite-sex faces reflected aesthetic judgments (i.e., "liking"), key-press behavior reflected the reward value of attractive female faces (i.e., "wanting"). Functional brain imaging (fMRI) procedures showed that passive viewing of beautiful female faces activated brain reward circuitry, in particular the nucleus accumbens in the ventral striatum. An extended set of subcortical and paralimbic reward regions also appeared to follow aspects of the key press rather than the rating procedures, suggesting that reward circuitry function presumably associated with enhanced mating motivation was activated by attractive opposite-sex individuals but not by attractive same-sex individuals (see Senior [2003] for a further discussion of these results).

Subsequent fMRI studies have provided further evidence that exposure to attractive faces stimulates activity in brain regions known to be involved in processing rewarding stimuli. O'Doherty et al. (2003) showed that activation of the medial orbitofrontal cortex occurred when subjects were not explicitly assessing faces for attractiveness, suggesting that the response is automatic. Although the effects of attractive faces on activation of the medial orbitofrontal cortex were similar in males and females and for both same-sex and opposite-sex faces, there was significantly greater activation in the ventromedial prefrontal cortex (a brain region implicated in affective-decision making and in responsiveness to sexual stimuli) in response to opposite-sex attractive faces in males than in females (O'Doherty et al. 2003; see also Winston et al. 2007). In a recent study, Tsukiura and Cabeza (2011b) showed that activity in the medial orbitofrontal cortex increased as a function of both attractiveness and goodness ratings, whereas activity in the insular cortex decreased with both attractiveness and goodness ratings. The authors argued

that their study provided evidence for a neural basis for the “beautiful is good” stereotype. Furthermore, in a related study, the same authors provided evidence that attractive faces not only capture more attention and interest, but also are easier to remember. Specifically, Tsukiura and Cabeza (2011a) reported that better memory for attractive faces reflects greater interaction between a region associated with reward, the orbitofrontal cortex, and a region associated with successful memory encoding, the hippocampus.

Taken together, the findings of several recent brain imaging studies have provided converging evidence that viewing faces of attractive opposite-sex individuals activates areas of the brain that are involved with reward. Further evidence for an association between exposure to attractive opposite-sex individuals and activation of mating motivation is provided by studies of mating motives in human social transactions and their underlying psychological and physiological mechanisms.

5.2. Mating motives in human social transactions and their psychological and physiological mechanisms

The evolutionary explanations of the effects of attractiveness on decision making in the labor market, in social transactions in everyday life, and in experimental economic games assume that when individuals engage in decision making in social transactions, multiple motivations may simultaneously be at play; some of these are related to obtaining resources (e.g., financial), whereas others may be social (e.g., status) or sexual. Just as financial considerations can drive decisions about partner selection for romantic and mating purposes, it should not be surprising that mating motives can influence economic decision making (e.g., Griskevicius et al. 2007). Given that sex can be a valuable commodity, mating and financial motives and goals are often closely intertwined in human social affairs.

5.2.1. Men. The notion that mating motives can influence economic decision making in men is supported by experimental evidence. For example, Wilson and Daly (2004) reported that exposure to photos of faces of attractive women induces men to prefer immediate smaller rewards over delayed larger rewards (see also Van den Bergh et al. 2008). Similarly, Van den Bergh and Dewitte (2006) reported that men who are primed with sexual stimuli are more willing to accept low offers in an ultimatum game, especially if these men have lower 2D:4D finger ratios (a marker of prenatal exposure to testosterone). These results suggest that exposure to attractive women activates men’s mating motivation and that such motivation enhances the desire for immediate rewards.

Evidence also exists about the potential psychological and physiological changes that occur in men following exposure to potential mates: These mechanisms can influence the evaluation of the potential benefits and costs of an ongoing or future interaction (therefore affecting decision making about this interaction), facilitate the expression of courtship behavior, and ultimately lead to favorable behavioral biases toward attractive individuals.

In a pioneering study, Roney (2003) reported that in men, exposure to women either in person or through photos can prime large changes in attitudes, mood, and self-perceived personality traits. These changes are such that men show

greater conformity to female mate preferences (e.g., preferences for men with resources who are willing to invest in their partners, through acts of generosity). Men exposed to women report higher valuations of material wealth, greater momentary feelings of ambition, higher valuations of indicators of high social status, and greater extraversion and generosity. These changes occur unconsciously. Roney (2003) argued that cues from potential mates prime psychological representations that facilitate the behavioral expression of courtship tactics. In subsequent studies, Roney et al. (2003; 2007) also showed that in men, a brief casual conversation with a moderately attractive woman produces an increase in salivary concentrations of testosterone (see also Van der Meij et al. 2008). Recently, Zilioli et al. (2014) reported that the mere exposure to faces of women (but not of men) increases men’s testosterone, regardless of the emotional expressions of these faces. Increased testosterone in men may enhance their behavioral courtship displays toward women, including humorous flirting, representing themselves in a favorable light, or displaying wealth, high social status, or generosity. As an example of this, it has been reported that male skateboarders who are being observed by an attractive woman experience an increase in testosterone and become more willing to display risky skateboard performances in front of the woman (Ronay & von Hippel 2010). Increased risk taking and other testosterone-associated attitudes in turn can influence financial decision making (e.g., Burnham 2007; Zak et al. 2009), and the decisions themselves can become courtship displays.

Further experimental evidence indicating the activation of men’s mating motives upon exposure to women comes from studies focusing on cognition and cortisol. Karremans et al. (2009) showed that interacting with women (but not with men) leads to a decline in men’s cognitive performance, as assessed with a working memory task. The more attractive the women, the stronger is the effect on cognition. Moreover, there was a negative correlation between performance management and cognitive performance, such that the more men invested effort in trying to make a good impression during the conversation, the worse was their subsequent performance on the cognitive task. The effect was interpreted as evidence of the cognitive costs of trying to make a good impression during the interaction. There were no effects of mixed-sex encounters on cognitive performance in women. In a follow-up study, it was shown that men’s cognitive performance (but not women’s) declined if they were led to believe that they interacted with a woman via a computer or even if they merely anticipated an interaction with a woman, suggesting that the effect can occur in the absence of a physical interaction with a woman and in the absence of any information about the woman’s attractiveness (Nauts et al. 2012). Again, these effects were interpreted as being the result of impression management efforts by the subjects. However, arousal-related mechanisms are also possible. When men have a brief casual interaction with a woman, there is an increase not only in their salivary testosterone, but also in their cortisol (Roney et al. 2010; Van der Meij et al. 2010). Cortisol concentrations are generally elevated in situations of high arousal, including sexual arousal (e.g., Goldey & van Anders 2012). Given that cortisol and other glucocorticoid hormones are known to influence cognitive function including spatial cognition, learning and memory, and working memory (e.g., de Kloet et al.

1999), cortisol may be a mechanism mediating the association between exposure to women and changes in cognitive function in men. Consistent with this hypothesis, an unpublished study by Zilioli and Watson (2014) demonstrated that men experience a cortisol increase after viewing photos of happy female faces; that they subsequently show a decrease in performance on a mental rotation task; and that the greater the increase in cortisol, the worse is the cognitive performance.

The effects of exposure to potential mates on physiology, self-perception, cognition, and decision making can potentially account for the tendency to show increased financial generosity or prosocial behavior toward attractive members of the opposite sex, even when such exposure is casual and very brief, when exposure occurs through photos of faces, and even in the absence of expectations of future interactions with the attractive individual. When a male employer has the opportunity to hire an attractive female employee, and therefore gain proximity to and familiarity with this individual for extended periods in the future, it is likely that the man's mating motivation is activated, consciously or unconsciously, regardless of his moral principles or intentions, and regardless of whether he will ever act on it. When a man is exposed to a photo of an attractive woman, it is likely that his mating motivation is activated regardless of whether the woman in the photo really exists and whether he will meet her in the future. The changes in physiology, self-perception, mood, and cognition that accompany the activation of sexual motivation by a potential mate occur regardless of conscious representations of goals or utilities, or knowledge of the probability of future interactions with the potential mate.

The human mind is equipped with mechanisms that are designed to trigger responses to specific cues, regardless of any conscious representations of goals or probabilities (e.g., Bargh & Chartrand 1999). For example, heterosexual males experience sexual arousal to pornographic images of women they will never meet and with whom they will never mate. Seeing a potential mate briefly in person or being shown his or her photo is likely to be sufficient to trigger the cognitive and physiological mechanisms regulating mating motivation and courtship behavior. These mechanisms may have a low activation threshold, especially in men, because of error management issues (Haselton & Nettle 2006), namely, the cost of missing a mating opportunity being greater than the cost of activating the mechanism when no mating opportunity is present. Moreover, these evolved mechanisms may treat novel stimuli, such as realistic visual images of attractive adults (or pornography), as veridical because the mechanisms are not prepared to make the distinction between real social stimuli and visual reproductions of these stimuli made with technology that has become available only recently. Furthermore, exposure to potential mates or their images is likely to activate the cognitive and physiological mechanisms regulating sexual interest and courtship behavior regardless of whether one is told that no further interaction with this person will ever occur. This is because during much of our evolutionary history, when humans mostly interacted with individuals that lived in the same geographic area and photos and computer screens had not yet been invented, any direct social interaction with a potential mate (or even a simple visual interaction) was likely to be followed by further interactions with this individual,

especially if the initial response to the potential mate was conducive to further interactions.

5.2.2. Women. Similar to men, women are biased toward attractive individuals as potential sexual partners, and this is especially the case in the initial stages of courtship and relationship formation (for evidence from speed-dating studies, see Kurzban and Wedeen [2005]). Similar to men, there is evidence that when women are primed with intersexual courtship they show an increased willingness to engage in risky behavior (e.g., Hill & Durante 2011). There is also evidence that watching a video showing an attractive man courting a young woman can increase women's testosterone and cortisol (Lopez et al. 2009). Although in men, simply interacting with women or viewing photos of their faces may release testosterone and cortisol, no study to date has shown that any interaction with men can trigger women's hormones. Such triggering, however, is not to be expected because the range of stimuli and situations that can activate mating motivation is more restricted in women than in men. A large body of research on men's and women's mating strategies has shown that women are more selective than men in their choice of mating partners and of the circumstances in which sexual interactions can take place (e.g., Buss 2003). In particular, although both men's and women's short-term mating strategies include pursuing casual sex with attractive partners, women are much more discriminating about the circumstances in which casual sex may take place than are men. For example, in a study in which campus students were approached by an attractive person of the opposite sex and asked a question – “Hi, I've been noticing you around town lately, and I find you very attractive. Would you have sex with me?” – 75% of men answered yes, whereas 0% of the women gave a positive answer (Clarke & Hatfield 1989).

When women's mating motivation is activated, however, it is likely that such activation is accompanied by physiological, psychological, and behavioral changes that promote female sexual courtship and render women more receptive to male courtship behavior. Some of these changes may be similar to those occurring in men, whereas others are likely to be different. For example, there is evidence that sexual thoughts, in the absence of any external sexual stimuli, can increase testosterone in women (Goldey & van Anders 2011). Increased testosterone in women, in turn, can influence risk taking and decision making (e.g., Bos et al. 2012). There is also evidence that women's increased sexual motivation driven by rising concentrations of estradiol during the peri-ovulatory phase of their menstrual cycle is accompanied by changes in self-perception; self-presentation; sociability; and interest in more attractive (e.g., more symmetrical) and more masculine features of men's faces, voices, and scents (Roney & Simmons 2013; Roney et al. 2011; Thornhill & Gangestad 2008). In general, although men's mating motivation is more dependent on external stimuli to be activated, women's mating motivation is more dependent on their reproductive condition and hormonal status (e.g., whether cycling or on contraceptives; pregnant; breastfeeding; and in the follicular, peri-ovulatory, or luteal phase of the menstrual cycle). In so far as women find physically attractive men appealing as potential mating partners and their mating motivation is active, one can expect positive behavioral biases toward attractive men similar to those displayed by men toward attractive women. These positive behavioral biases may

also include employment or career advancement decisions, or allocation of financial resources in the labor market and in experimental economic games. Important sex differences in mating motivation and mating strategies, however, may result in the effects of attractiveness on decision making being more consistent, and perhaps also stronger, in men than in women. Sociocultural factors are likely to contribute to this sex difference as well.

6. Development of attractiveness-related biases

Preferences for attractive faces begin very early in life, as 2- or 3-month-old infants look longer at attractive than unattractive faces of adults (Langlois et al. 1987). In their meta-analysis of the attractiveness bias literature, Langlois et al. (2000) examined possible age effects on the reliability of attractiveness ratings and in the judgment and treatment of attractive individuals by children aged 6 years and older. They found no significant effects of age and concluded that attractiveness is as important for children as for adults (e.g., see Dion 1977). Agthe et al. (2013), however, showed that at the time of puberty there is a sharp increase in the extent to which adolescents display a positive bias toward attractive opposite-sex targets (who are potential mates) and a negative bias toward attractive same-sex targets (who are potential sexual rivals), indicating that important changes in attractiveness-related biases occur when mating motivation is strongly activated by pubertal hormonal changes.

Although there is no experimental research on this topic, it is likely that the neural and psychological mechanisms underlying positive biases toward attractive individuals are already present shortly after birth, even though these biases may have no immediate functional significance in the infants' social world. Selective attention to attractive faces early in life and social preferences for attractive individuals during later stages of development (e.g., Dion 1973; Dion & Berscheid 1974), however, may facilitate the expression of biases that are functional and adaptive later in life; for example, it is possible that greater selective attention to attractive faces in infancy is associated with greater positive biases toward attractive opposite-sex individuals after puberty.

The association between being attractive and receiving favorable treatment from others also begins very early in life. There is evidence that adults direct more attention and more positive behavioral responses to attractive ("cute") young infants, both males and females (Hildebrandt & Fitzgerald 1978; Karraker 1986; Ritter et al. 1991). Mothers, too, appear to be more favorably biased toward their more attractive babies (Langlois et al. 1995; Rieser-Danner et al. 1987; see Leinbach and Fagot [1991] for older children). Furthermore, it has been shown repeatedly that schoolteachers have more positive expectations about the academic performance of attractive male and female children and adolescents and treat them more favorably (Babad et al. 1982; Barocas & Black 1974; Berkowitz & Frodi 1979; Clifford & Walster 1973; Dion 1974; Felson 1980; Kenealy et al. 1987; Lerner et al. 1990; Mohr & Lund 1933; Murphy et al. 1981). Finally, more attractive children and adolescents are more popular with their peers (Dion & Berscheid 1974; Dion & Stein 1978; Felson & Bohmstedt 1979; Kleck et al. 1974; Lippitt 1941; Ritts et al. 1992; Smith 1985; Vaughn & Langlois 1983; Weisfeld et al. 1983; 1984).

Preferential treatment of attractive infants and young children by their own parents can be explained, from an evolutionary perspective, with the differential parental solicitude model (Daly & Wilson 1995). According to this model, if attractiveness is an indicator of genetic or phenotypic quality, parents should invest more in attractive than in unattractive children (see also Langlois et al. 2000). Because adults can respond parentally toward children who are not their biological offspring, the differential parental solicitude model can also explain the favorable biases toward attractive infants and young children expressed by adults who are not their biological parents. In terms of mechanisms, a number of studies have shown that perceptual biases exist in human minds that make infant faces attractive to older individuals (in children older than 6 years, adolescents, and adults; for evidence that these biases are stronger in females than in males, see Maestripieri and Pelka [2002]), that visual and auditory responsiveness to infants is regulated by areas of the brains involved in reward (Glocker et al. 2009), and that interest in infants is upregulated by estrogen in women and downregulated by testosterone in men (Law Smith et al. 2012; Zilioli et al. 2016). Presumably, the same mechanisms responsible for positive biases toward infants in general are also responsible for greater biases toward attractive than unattractive infants.

As children grow older and become objects of romantic interest and, at around the time of puberty, also of sexual interest to other children, it is likely that attractive children who early on stimulated greater parental motivation and investment later elicit greater romantic and sexual interest. The transition from being the recipient of parental investment to being the target of sexual interest presumably occurs at earlier ages for girls than for boys, in relation to girls' earlier timing of puberty and to the notion that males value young age in potential mates more than do females (e.g., Buss 2003). Because the regulation of mammalian parental and mating motivation has been quite conservative from an evolutionary perspective (e.g., in females, estrogen acts in the same brain region, the preoptic area of the hypothalamus, to regulate both parental and sexual motivation) (Saltzman & Maestripieri 2011), one may speculate that the same neural and neuroendocrine mechanisms that regulate perceptual and behavioral biases toward attractive children from a parental motivation perspective also regulate perceptual and behavioral biases toward attractive adolescents and adults from a mating motivation perspective. Positive biases toward attractive children and attractive adults may essentially be the same phenomenon, which acquires different functional significance in different contexts. Therefore, evolutionary explanations, coupled with our knowledge of the physiological regulation of motivation, can potentially account for favorable biases toward attractive individuals across the life span, from the earliest manifestations of these biases toward attractive infants to later manifestations of biases toward attractive middle-aged and elderly individuals (for sex differences in perceived attractiveness of middle-aged individuals, see Maestripieri et al. [2014]).

7. Conclusions, limitations, and future directions

In the real world, decisions made in social transactions between two or more individuals, whether they involve money, are generally affected by the characteristics of the

individuals and by the context in which the transactions occur. The same is true about decisions made in experimental economic games when the players' identities are known and regardless of whether these decisions involve donating or sharing money, or investing in others in hopes that they will reciprocate. In both the real world and in the laboratory, people are often biased in favor of attractive individuals. These effects of attractiveness on decision making have baffled economists for decades because they are not predicted by their rational models of human behavior. The effects of attractiveness on decision making have also attracted the interest of social psychologists and of evolutionary psychologists, who have attempted to explain these effects using the conceptual tools of their discipline.

Although many would agree that financial and prosocial biases in favor of attractive people probably have multiple determinants, economists and social psychologists attempting to explain these biases often ignore the role of mating motivation (but see Langlois et al. [2000] as an important exception). Whether physical attractiveness is correlated with particular personality traits, prosocial behavior, professional competence, or productivity remains an open question. Evolutionary psychologists, however, recognize that physical attractiveness has intrinsic value and it is not simply a marker of behavior. Therefore, there is an incentive to invest in attractive people because of their high mate value, regardless of their psychological or behavioral characteristics. Moreover, the human mind is probably predisposed to respond to cues of mating and activate courtship behaviors regardless of any conscious awareness of goals, incentives, or probabilities of future gains.

The effects of attractiveness on financial and prosocial biases are often moderated by the sex of the target (i.e., the attractive person who benefits from biased financial and prosocial behavior) and the sex of the actor (i.e., the person who expresses biased behavior in favor of the attractive individual). The importance of sex has been highlighted by laboratory studies involving experimental economic games and by field and laboratory studies of the labor market, whereas a previous meta-analysis of studies of attractiveness-related biases in social psychology did not report significant sex effects (Langlois et al. 2000). If future empirical studies or reviews of the literature fail to confirm that financial and prosocial biases toward attractive people are stronger in opposite-sex than in same-sex interactions, this would indicate that the evolutionary models of attractiveness-related biases are limited in their ability to account for this phenomenon in its entirety and that other explanatory models, not involving sexual attraction and mating motivation, should be taken into serious consideration. Similarly, future research on positive biases toward attractive children and adolescents may also highlight the limitations of evolutionary models in explaining all attractiveness-related biases if such research were to show that positive biases toward children and adults are regulated by different mechanisms (e.g., if the biases toward children are entirely driven by differences in behavior between attractive and unattractive children). It is unlikely, however, that future empirical studies or reviews of the literature would come to the conclusion that mating motivation plays a trivial role in the genesis of financial and prosocial biases toward attractive individuals and that this factor can be safely ignored by economists and social psychologists, the way they ignored it in the past. Future studies

examining the hypothesis that attractiveness-related financial and prosocial biases are driven by mating motivation could test novel predictions of this hypothesis: For example, there should be a stronger bias if the attractive target is romantically available (e.g., single) or sexually receptive (e.g., he or she has an unrestricted sociosexual orientation). Cultural differences in the strength of biases could also be expected, depending on how common sexual promiscuity is within a culture.

Recognizing the important role of mating motivation in financial and prosocial decision making implies that knowledge of the factors that lead to variation in mating motivation among different individuals or among the same individuals over time or in relation to context is highly relevant to understanding interindividual and intra-individual variation in decision making. Because evolutionary psychologists have in the past few decades accumulated an impressive body of knowledge about human mating motivation, this body of knowledge should be increasingly connected with research on financial decision making (e.g., Wilson and Daly [2004] is an early example of this).

Evolutionary approaches to human behavior emphasize its functional significance (i.e., the notion that humans evolved psychological predispositions and behavioral preferences that maximize biological fitness). Recognition of the functional significance of behavior or preferences is often absent from models developed by economists and psychologists (see Burnham 2013). Evolutionary perspectives can therefore complement the theoretical perspectives adopted by other behavioral scientists who focus their attention on similar phenomena. This is especially the case when these phenomena include biases in behavior and decision making associated with evolutionarily meaningful human biological characteristics such as physical attractiveness.

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Open Peer Commentary

Strong but flexible: How fundamental social motives support but sometimes also thwart favorable attractiveness biases

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Abstract: Research corroborates the notion that fundamental social motives play an important role in biases that favor attractive people. Although an adaptationist framework expects favorable social effects of good looks in most situations and contexts, it simultaneously allows for potential negative social reactions and outcomes that may be elicited by physical attractiveness in other contexts. These effects of attractiveness reflect the reproductive opportunities and threats posed by potential mates and rivals.

Maestripieri et al. provide a valuable conceptual framework for understanding social biases associated with physical attractiveness. Although an adaptationist framework predicts positive social effects of physical attractiveness in some contexts, it also predicts negative social effects of attractiveness in other contexts. Moreover, there are important boundary conditions in how, when, and toward whom those biases are expressed. These patterns reflect the reproductive opportunities and threats posed by potential mates and rivals.

The biasing effects of attractiveness (Talamas et al. 2016) are consistent with humans' natural attention to beauty (Maner et al. 2007b; Mo et al. 2016; Sui & Liu 2009). This preference for good looks is shaped by natural selection and linked to the perception of the target's reproductive value (cf. "good genes theory"; Hamilton & Zuk 1992). People tend to react positively toward attractive members of the opposite sex, reflecting a heightened desire for social interaction (Lemay et al. 2010). In line with evolutionary principles, positive biases toward good-looking persons emerge because attractive people on average have high reproductive value and hence are desired as potential mates.

Consistent with sexual strategies theory (Buss & Schmitt 1993), attractive faces of one's preferred sex are processed with a higher responsiveness in the reward circuitry of people's brains (Kranz & Ishai 2006). Women and men elicit stronger neural responses when viewing faces of desirable mates (Cloutier et al. 2008; Ishai 2007).

Reactions to attractive persons depend on their sex and one's sexual preference (Försterling et al. 2007). Moreover, those reactions are consistent with the fundamental social motives framework, which posits that human motivational systems are functionally shaped to manage the relevant opportunities and threats afforded by social life (Kenrick et al. 2010; Neel et al. 2016). Adaptive mating-related biases (facilitating access to potential mates and avoiding potential rivals) may guide different reactions to attractive other-sex versus same-sex persons.

Indeed, physical attractiveness sometimes leads to negative, rather than positive, interpersonal judgments and outcomes. In the context of social relationships, people often perceive attractive same-sex persons as a threat to their self-esteem (Park & Maner 2009), mate value (Gutierrez et al. 1999), and partnership, as well as reproductive success (e.g., Buss et al. 2000). The presence of intrasexual competition is linked to the activation of mate-guarding motives (Maner et al. 2009b; 2012) and even occurs automatically and without awareness (Massar & Buunk 2010). As soon as people reach sexual maturity (Agthe et al. 2013), they tend to derogate (Schmitt & Buss 1996; Vaillancourt 2013) and avoid (e.g., Agthe et al. 2008; 2011; Luxen & van de Vijver 2006) attractive same-sex persons. Accordingly, attractive female adolescents are at greater risk for indirect victimization (Leenaars et al. 2008). Women are often surrounded by friends who are similar in attractiveness, and less attractive friends tend to perceive more mating rivalry (Bleske-Rechek & Lighthall 2010). As women compete more on the dimension of physical attractiveness than men do (Dijkstra & Buunk 2002), women are particularly intolerant of "sexy peers" (Vaillancourt & Sharma 2011).

Negative reactions toward attractive same-sex persons are displayed particularly by people who are likely to fear intrasexual competition: for example, people in their young adulthood (Agthe et al. 2013) who tend to be only moderately attractive themselves (Agthe et al. 2010; Bleske-Rechek & Lighthall 2010), have relatively low self-esteem (Agthe et al. 2011) and high levels of chronic jealousy (Maner et al. 2009b), and tend to

compare downward to avoid social comparison threat (Agthe et al. 2014). Concerns associated with self-esteem and social comparison reflect proximate manifestations of underlying adaptive mating-related motives.

Similarly, boundary conditions for advantageous attractiveness-based biases should be considered. For example, favorable reactions toward attractive opposite-sex targets are less likely when perceivers are involved in dating relationships (Simpson et al. 1990). In a committed partnership, people sometimes ignore (Maner et al. 2008; 2009a) or devalue (Lydon et al. 2003) attractive alternatives. Conversely, attentional attunement to attractive women is pronounced in sexually unrestricted men (Maner et al. 2007a), and nonexclusive daters tend to judge attractive available targets more favorably than unavailable ones (Bazzini & Shaffer 1999). When women are in the fertile phase of their menstrual cycle, they respond more positively toward attractive men (Haselton et al. 2007), while displaying negative and competitive reactions toward attractive women (Fisher 2004). In addition, attractiveness-based biases emerge almost exclusively toward targets of the evaluator's own ethnic background (Agthe et al., 2016). Culture, family expectations, kinship rules, and the extent of individual choice that is allowed in personal relationships may also affect attractiveness-based biases (Anderson et al. 2008; Yu & Shepard 1998).

In sum, prior findings are consistent with the notion that mating-related motives play a role in people's reactions to good-looking persons and point to neural and evolutionary underpinnings of attractiveness-based biases. Physical attractiveness can produce both positive and negative social biases that vary with features of the perceiver (e.g., mood, hormonal influences), the target person (e.g., age, status), and the social context. Such biases reflect fundamental affordances associated with mating and involve motivational systems linked to seeking mates and competing with intrasexual rivals.

Attractiveness biases are the tip of the iceberg in biological markets

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Abstract: Physical attractiveness affects how one gets treated, but it is just a single component of one's overall "market value." One's treatment depends on other markers of market value, including social status, competence, warmth, and any other cues of one's ability or willingness to confer benefits on partners. To completely understand biased treatment, we must also incorporate these other factors.

The target article by Maestripieri et al. is a nice example of how people's market value affects others' willingness to help, hire, or otherwise confer benefits on them. The target article defines "market value" as one's physical attractiveness, but one's overall market value need not be limited to the mating domain. Because sexual selection is part of social selection more generally (Lyon & Montgomerie 2012; West-Eberhard 1979; 1983), mate choice is also a subset of partner choice more generally, where organisms choose whom to interact with for either sexual or non-sexual relationships. Hence, mates (or potential mates) are just one type of partner that people can choose, albeit a very important type. This commentary generalizes the points in the target article beyond physical attractiveness and mating potential.

Biological markets theory describes how organisms choose partners (Noë & Hammerstein 1994; 1995). It treats social

interactions as occurring within a “market” for commodities, where some individuals are more desirable partners because of their greater ability, willingness, or availability to confer benefits upon partners (Barclay 2013; 2015; 2016). For example, in the mating domain, some partners are healthier, more fertile, more receptive, or better parents, or they carry “good genes” that offspring will inherit. Courting someone with these traits will statistically increase one’s fitness, so we evolved to be sexually attracted to cues of these traits. In nonmating domains, some partners provide more effective or more frequent aid, coalitional support, food, knowledge, skills, and so on; these commodities provide statistical fitness benefits, so we evolved to be socially attracted to them. One’s overall “market value” in any domain is a composite of one’s relative desirability based on the relevant traits, just as one’s “mate value” is one’s relative desirability based on mating-related traits alone.

Many principles that apply to mating relationships will also apply to nonmating relationships. For example, the target article shows that people are biased toward physically attractive individuals (high mate value) because it is more beneficial to attempt to mate with them. People are also biased toward individuals with other types of market value (i.e., other cues of ability or willingness to confer benefits). For example, high-status people receive preferential treatment in many domains, such as being listened to more often, receiving disproportionate shares of group productivity, and being excused from some social obligations or for bad behavior (reviewed by Henrich & Gil-White 2001; Kafashan et al. 2014). People who appear competent are preferentially chosen as partners for tasks, from job searches to schoolyard team picking; competence-based choice occurs in chimpanzees (Melis et al. 2006) and even in trout (Vail et al. 2014). People who appear wealthy elicit more compliance with their requests (e.g., Nelissen & Meijers 2011). People who appear altruistic or trustworthy are chosen more often as cooperative partners (e.g., Barclay 2004; 2006; Barclay & Willer 2007; Cuesta et al. 2015; Gallo & Yan 2015), selected as leaders (Milinski et al. 2002), and even preferred as romantic partners (e.g., Arnocky et al., *in press*; Barclay 2010). So although biases toward physically attractive people are important, they are the tip of the iceberg in terms of preferential treatment toward people with high market value. Future research should compare the relative importance of different market-related traits, such as how people trade off the physical attractiveness of (supposedly nonromantic) partners against their competence, status, wealth, cooperativeness, and so on.

Biological markets theory allows us to make further predictions about attractiveness biases, or indeed any biases toward people with high market value. First, the magnitude of bias for a given trait depends on supply and demand. Attractiveness biases should be higher in environments where physical attractiveness is in high demand or low supply, for example, because of high pathogen pressure (Gangestad & Buss 1993) or when other needs like resources are relatively less important (Marlowe 2003). There will be stronger biases toward wealthy people when resources are crucial, toward physically proficient people when physical coalitional conflict is common, and so on.

Second, the magnitude of any bias depends on the variance in that trait. It is pointless to choose partners based on traits with no variance. Choosiness about cooperators diminishes when most people are cooperative (McNamara et al. 2008), so attractiveness should matter less in environments where everyone is attractive, wealth should matter less when everyone is wealthy, and so on.

Third, biases for particular traits depend on people being able to potentially “consume” it. Single men should display larger biases toward attractive women than do married men, especially in strictly monogamous societies with few extra-pair matings (less so under polygyny). Attractiveness should be less important if the target is married, raising children, sexually unreceptive, or chaste. People who do not need a particular trait in a partner should display lower biases toward others who possess it, such

as people who do not need a partner’s help being less cooperative (Barclay & Reeve 2012; Kafashan et al. 2014).

Fourth, people who themselves have high market value should be more discriminating (e.g., more influenced by attractiveness) because they are more likely to succeed at attracting the desirable partners than would a low market value person (e.g., Little et al. 2001). For example, attractive men should show stronger biases toward attractive women, good cooperators should show stronger biases toward cooperators, and so on. High market value in one domain can predict preferences in others, such as wealthy individuals showing stronger biases toward attractive partners or vice versa. Extremely unattractive individuals may even be biased against attractive people, whom they have no hope of attracting.

I have highlighted four general types of predictions, derived from biological markets theory, about attractiveness biases. This list is limited by space, not by the utility of the theoretical perspective. Maestriperi et al. have nicely documented biases toward people possessing one highly salient market-related trait (physical attractiveness); we look forward to further work on other market-related traits, how these biases vary with social and ecological circumstances, and the relative weight of each trait across situations.

Attention and memory benefits for physical attractiveness may mediate prosocial biases

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Abstract: Mating motivations can explain attractiveness benefits, but what proximate mechanisms might serve as efficient causes of these biases? There is growing evidence that visual cues of physical attractiveness capture attention and facilitate memory, enhancing salience in ways that could underlie, for example, preferring one job applicant over another. All of these effects beg deeper questions about the meaning of attractiveness.

Empirical evidence for the benefits of being attractive is not easily dismissed, and I agree with the authors that we cannot ignore the explanatory role played by deep-seated mating motivations. However, ancestral mating success is an ultimate cause; one also needs to ask what proximate mechanisms might give rise to these biases and how “attractiveness” is defined in facial signal detection.

The financial/prosocial benefits that the physically attractive enjoy may arise from overt mating strategies that seek to continue interaction with attractive others. However, the salience of one job applicant over another, or the selection of an interaction partner in an economic game, could also arise, at least in part, from cognitive processing biases that can be found in the developmental and evolutionary literatures. Physically attractive women and men have been shown to grab our attention (e.g., Maner et al. 2003), an effect that appears in infancy, replicates across race and age of the faces (Langlois et al. 1991), and cannot simply be reduced to symmetry detection (Samuels et al. 1994). In contrast, memory appears to be sensitive to better recognizing only attractive females, not males (e.g., Becker et al. 2005). These effects follow naturally from the perspective that certain features of attractiveness correspond to signs of genetic health and fertility, and that these have different values for short- and long-term mating goals as a function of observer sex.

Attention to attractiveness may be instrumental to adult mating success, but why should infants prefer attractive faces? From the evolutionary-developmental perspective, mating motivations should promote attentional vigilance to signs of genetic fitness even in children without mature mating motivations, because

such attention facilitates the building of internal representation systems that will later form the multidimensional “mating space.” The resulting representational system can then, at the onset of puberty, facilitate both mate pursuit and mate acquisition, as well as promote an awareness of one’s own mate status, the recognition of reciprocal mating interest, and vigilance to same-sex competitors with the greatest ability to poach our romantic partners. Adult attention is hence a symptom of long-standing habits of adaptive information pickup of mating affordances.

Although physically attractive male and female faces both garner more attention, the long-term encoding of individuating features favors attractive women, but not men (who are more likely to be confused with one another; e.g., Becker et al. 2005). Sex differences in the fitness value of physical attractiveness cues suggest an explanation for this disjunction. Short-term mating goals (i.e., those focused on genetic quality and de-emphasizing long-term resource provisioning and parental investments) are sufficiently served by attention being drawn to cues of genetic fitness. Long-term mating strategies must additionally track signs of cooperative and committed behavior for the same individual over time, necessitating a more individuated memory code. Women are more likely to embrace long-term strategies because of sex differences in parental investment, and accordingly, male mate value is more tied to things like status and resources (Buss & Schmitt 1993). Such differences collude so that a man’s physical attractiveness does not inspire as much encoding into memory without further information. Fluctuations in mating motivations should enhance these effects. For example, ovulating women show increases in attention to attractive men, but no such benefits in memory (Anderson et al. 2010). Such findings must be tempered by evidence that women’s definition of male facial attractiveness changes during ovulation, emphasizing more masculine (i.e., testosterone-related) features (Boothroyd et al. 2008). Considerable work remains to tease out how these features differentially resonate in cognitive processing. Such considerations suggest a number of testable predictions for sex differences in employee evaluation and economic cooperation games.

The memory difference could also arise from properties of the signal itself. Consider the female-carrier hypothesis (Salter 1996), which suggests that certain female facial features are attractive because they facilitate paternity certainty for male mates, allowing the father’s features to show through more clearly in the offspring. Such features would additionally differentiate attractive women from each other, working against the “attractiveness is prototypicality” claim (as reviewed in Little et al. 2011) and providing additional cues promoting better memory for the female faces that will most likely facilitate paternity determinations. Indeed, the morphed prototypical average of attractive female faces is noticeably different from the morphed average of all female faces (Perrett et al. 1994), suggesting that these faces have additional features for which recognition could be vigilant. In contrast, male facial attractiveness may be much more about prototypicality, which undermines discriminability in memory. Whereas hormone markers should drive attentional vigilance, features that facilitate paternity certainty, which are at their basis about recognition, should translate into better recognition memory.

These cognitive effects could be largely automatic and could readily produce biases in hiring, and so forth, even when proximity/mating is not an explicit goal. If attractiveness is understood as a set of visual signals of mate quality, this grounds the meaning of attractiveness in mating-related instincts and yields falsifiable explanations of both attention and memory effects, which contribute to the behavioral biases discussed in the target article. This also yields a reciprocal grounding of unattractiveness, and we should be open to the possibility that some of these behavioral effects may be more about evolved mechanisms for avoiding socially costly (e.g., unhealthy) coalition partners.

I have focused on face perception here, largely because that is where the data are available. However, physical attractiveness is also body, movement, voice, smell, and other things. Future

work should examine the degree to which the varying features of attractiveness differentially predict mating success and relate these more concrete factors to the variance for which they account in differential employment and cooperation outcomes.

There is more: Intrasexual competitiveness, physical dominance, and intrasexual collaboration

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Abstract: It is emphasized that in organizational settings, the responses to same-sex attractive others are enhanced among individuals high in intrasexual competitiveness; that especially attractive rivals who are perceived as unfriendly will induce competition; that among males, physical dominance may induce more competition than physical attractiveness; and that especially males may prefer to associate with attractive same-sex others for intrasexual collaboration.

Maestriepieri et al. present an analysis that is long overdue by examining the evolutionary bases of why and when people would, and more importantly, would *not*, respond positively to attractive others in what I would refer to as work-related contexts. I agree largely with the conclusions of Maestriepieri et al., but would like to substantiate and complement their analysis in a number of ways.

To begin with, research on assessing the motives underlying the responses to attractive others may benefit from including the scale for intrasexual competitiveness (ISC;) (Buunk & Fisher 2009). This scale measures the desire to be preferred by opposite-sex others rather than by same-sex others, the desire to view oneself as better than same-sex others, envy and frustration when same-sex others are better off, and overall negative feelings toward same-sex others. In various experiments, we have demonstrated the role of ISC in work-related contexts. For example, in one experiment we had female participants perform a series of tasks during which their own picture, as well as that of a rival, was visible on the screen (Buunk et al. 2016). We created a realistic situation of competition for a job promotion because, after passing the test period, the alleged supervisor would choose one of the two students for a job. An attractive rival induced more jealousy overall, and she reduced the career expectations particularly of women high in ISC.

This experiment was also theoretically relevant to the present discussion for another reason. Although most studies in social psychology have considered attractiveness as a one-dimensional variable, and have assumed that attractive people are in general viewed in positive terms, our results suggest that the attractiveness of a rival can have rather distinct effects depending on the way in which her personality is perceived. That is, we found that especially when the attractive rival was perceived as unfriendly, she induced high levels of jealousy and low career advancement expectations (Buunk et al., in press 2016). Hence, an attractive individual may evoke more jealousy and may be perceived as a more serious threat to one’s career when she is perceived as a rather “nasty” individual.

Although, as highlighted by Maestriepieri et al., physical attractiveness may play an important role in work-related contexts, I would like to suggest that physical dominance may play a role of equal importance in such contexts. First, many studies have highlighted the advantages that tall people have in task-related settings. As they are taller, people are more likely to emerge as leaders and are more likely to influence others. For example, Stulp et al. (2015) had participants rank 12 items (e.g., extra clothing, a pistol, a compass) on importance for the “Arctic survival task.” Subsequently,

they were at random assigned to a same-sex other with whom they were instructed to rank the items again as a team. Relatively taller individuals had a larger influence on the joint rankings, although only when the difference between initial rankings was large.

Second, in line with studies on jealousy in intimate relationships (e.g., Dijkstra & Buunk 2002), in a study by Buunk et al. (2010), each participant was confronted with a scenario in which one's the supervisor seemed to like one's the participant's co-worker more. The physical dominance of the rival appeared to arouse more jealousy in men than in women, whereas the physical attractiveness of the rival appeared to arouse more jealousy in women than in men. This sex difference was found especially among those high in ISC (Buunk & Fisher 2009) who were confronted with a same-sex supervisor. Hence, intrasexually competitive females with a female supervisor tended to feel particularly jealous when their colleague was physically attractive, and intrasexually competitive males with a male supervisor tended to feel particularly jealous when their colleague was physically dominant. These findings suggest that intrasexual competition has a sort of dynamic of its own and may be induced more by the presence of same-sex others than by the presence of opposite-sex others (cf. Campbell 2002; Geary 1998).

Finally, in addition to mating and intrasexual competition as motives that may underlie the responses to physically attractive others, there is a third motive, which seems to have been overlooked in the literature. Under certain conditions, intrasexual competition may be superseded by the perceived benefits of intrasexual *collaboration*. In a recent study addressing this issue (Buunk & Massar 2014), we argued that to attract potential mates, people may associate with same-sex others who are even more attractive to the opposite sex than they themselves are. We reasoned that this would apply particularly to men. Therefore, more than women, men would prefer the company of physically attractive and socially dominant companions in a mating context (in this study going to a party) more than in a neutral context (in this study going to a movie). We found that both sexes preferred a more attractive companion in the mating than in the neutral context. However, in the mating as compared to with the neutral context, men, but not women, found the attractiveness of a companion more important, preferred a more socially dominant companion, and found the social dominance of a companion more important. Hence, especially men's attitude toward same-sex others in a mating context may be driven by the desire to associate, rather than to compete, with same-sex others who are attractive to the opposite sex. Although work settings are not primarily mating contexts, as the analysis by Maestriperieri et al. suggests, mating motives may often play a role in work settings.

To conclude, the analysis by Maestriperieri et al. is timely and theoretically very important, but future research in organizational settings might also pay attention to the role of individual differences in intrasexual competitiveness, to different perceptions of attractive others (especially his or her unfriendliness), to the role of height and physical dominance, and to the role of intrasexual collaboration in addition to intrasexual competition.

Explanations for attractiveness-related positive biases in an evolutionary perspective of life history theory

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Abstract: The mating-related evolutionary explanation that Maestriperieri et al. offer does not apply to (1) infants' positive biases toward attractive

individuals and (2) adults' positive biases toward attractive infants and children. They are best understood when integrated into an evolutionary life history framework. I argue that the life history of positive biases toward attractive individuals is driven by fundamental trade-offs made throughout development.

The target article provided an evolutionary account for the financial and prosocial biases in favor of attractive people. Within the framework of a mating-related evolutionary model, Maestriperieri et al. argued that the mating motivations lead to a strong bias in favor of attractive individuals in adults. However, this evolutionary model did not explain the development of attractiveness-related biases in section 6 in the target article – that is, (1) children's positive biases toward attractive individuals (including same-age peers and adults) and (2) adults' positive biases toward attractive children. In this commentary, I integrate the ideas about the mating-related evolutionary model with another evolutionary theoretical model (i.e., life history theory), which may provide different functional explanations for the positive biases in favor of attractive people.

Life history theory examines how evolved mechanisms affect development throughout the life span (Del Giudice et al. 2015; Griskevicius et al. 2011; Hill & Kaplan 1999). Natural selection produces development-related energetic and resource allocations between somatic effort (i.e., the growth and maintenance of one's body) and reproductive effort (i.e., mating and caregiving). An optimal life history trade-off is resolved by the coordinated tuning of multiple physiological (e.g., endocrine, hemostasis, and immunity) and psychological (e.g., behavior, cognition, and attitude) systems, which constantly assess environmental constraints and accordingly calculate the energetic allocations (Del Giudice et al. 2015). As an example, physical attractiveness can be seen as adaptive strategies in response to different environmental challenges inherent in the life history traits (Sugiyama 2015). Attractiveness-related social judgment biases may reflect different fitness-promoting aspects of social motives over the life span (Kenrick et al. 2010).

First, given that individuals before puberty have no mating motivation, the mating-related evolutionary model by Maestriperieri et al. did not explain why they still have positive biases toward attractive people. According to the life history theory, in infancy and childhood, survival is the main task and challenge (Bogin 1997; Bowlby 1969; Chen & Chang 2012). So immature individuals' preferences for attractive faces represent a self-protection strategy to increase their opportunity for survival, because attractive faces commonly indicate less danger (Rhodes 2006). For example, adults with attractive faces are perceived to afford more warmth, honesty, and naïveté and less danger than those with less attractive faces (Berry & McArthur 1986; Berscheid & Walster 1974). Because of the importance of the fitness-relevant information conveyed by attractive faces, the positive biases in favor of attractive people may have been selected in young infants.

Second, I question the prediction by Maestriperieri et al. that greater attractiveness-related positive biases in infancy might be linked to greater positive biases toward attractive opposite-sex individuals starting from adolescence. The latter may reflect underlying motives associated with mating. It seems to suggest that infants' preference for attractive faces may be functionally prepared for the expression of biases to fulfill mating-relevant goals later. However, the existing evidence suggests that their hypothesized effects are rather weak. I argue that the attractiveness-related biases in infancy may reflect underlying motives associated with survival/self-protection rather than mating. To give an example, infant preferences for attractive faces are apparent for strangers' faces (Langlois et al. 1990). Specifically, infants show higher levels of withdrawal and distress toward an unattractive stranger, whereas they show higher levels of positive affection and interactions with an attractive stranger. This means that selective preferences for attractive faces when infants interact with a stranger can represent one of the behavioral strategies activated by the attachment behavioral system to promote safety and survival. However, it should be noted that such selective preferences

are not likely to affect infant behavior toward familiar caregivers because of the importance of the attachment relationships between infants and familiar caregivers (Langlois et al. 1990).

Given the different evolutionary functions underlying the biasing effects of attractiveness, the life history model also explains age differences in attractiveness biases toward opposite-sex and same-sex individuals over the life span. For example, there is no clear evidence for positive attractiveness biases toward opposite-sex people in infant and childhood (Dion 1973; Langlois et al. 1991; Saxton et al. 2006). However, starting from adolescence, mating is the main goal. Therefore, there is a rapid increase in positive biases toward attractive opposite-sex people in adolescence (Agthe et al. 2013). These sexually mature individuals' preferences for the attractive opposite-sex face represent a strategy to increase their opportunity for reproduction (Kościński 2011), because physical attractiveness is an indicator of overall quality, including greater genetic quality, as discussed in the target article. The age changes in attractiveness-related biases further reflect the fundamental life history trade-offs between somatic and reproductive effort.

Last, given that adults have positive biases toward attractive children not because of their mating motivation, the mating-related evolutionary explanation by Maestripieri et al. is obviously inappropriate. However, according to the life history model, adults (especially parents) may invest more in attractive than in unattractive infants because infant attractiveness may signal health and competence (Rhodes et al. 2001b; Ritter et al. 1991), which may consequently enhance adults' reproductive fitness (Beaulieu & Bugental 2008). A large and convergent body of literature (e.g., Allen et al. 1990; Barden et al. 1989; Field & Vega-Lahr 1984) indicates generally that compared with parents of normal children, parents of children with various types of congenital anomalies (mainly craniofacial anomalies) showed more negative parental behaviors (e.g., controlling) and fewer positive parental behaviors (e.g., responsiveness and warmth). Even in the normal sample, mothers showed higher levels of positive interactions with more attractive infants compared with less attractive infants (Langlois et al. 1995). Therefore, these studies all suggest that parental differential preference and investment in their children as a function of cues to the child's reproductive value may reflect their life history trade-off.

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Is there an alternative explanation to the evolutionary account for financial and prosocial biases in favor of attractive individuals?

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Abstract: All three critical points of the evolutionary explanation proposed by Maestripieri et al. may not withstand close scrutiny. Instead, there should be an alternative explanation that has nothing to do with genetic continuity, but stresses the rewarding property of attractiveness that results mainly from sociocultural value assignment and sexual experience pursuit.

After comparing explanations provided by economists, social psychologists, and evolutionary psychologists, Maestripieri et al. concluded that the evolutionary explanation best accounts for

financial and prosocial biases in favor of attractive adults. According to the evolutionary explanation, these biases occur because attractiveness (1) indicates higher biological fitness such as health and fertility and (2) hence could activate mating goals, consciously or unconsciously, and (3) for a functional purpose of reproducing offspring with greater genetic quality. Although acknowledging the thoroughness of their review from an interdisciplinary perspective, I suggest that all three critical points of the evolutionary explanation proposed by Maestripieri et al. may have difficulty in standing up to scrutiny.

First, although the authors cited several articles to support the idea that "human facial attractiveness is likely to be an indicator of overall quality" (sect. 2.1.3, para. 2), there was plenty of evidence suggesting no relationship between attractiveness and biological fitness (e.g., Gray & Boothroyd 2012; Kalick et al. 1998; Shackelford & Larsen 1999; Weeden & Sabini 2005). Actually, the most recent review article cited by Maestripieri et al. also concluded that the supporting evidence was far from strong (Rhodes 2006). Therefore, the indicating effect of attractiveness could at most be considered as a pending issue or might only exist in certain environments (Hunt et al. 2004). Interestingly, although females' waist-to-hip ratio (WHR) is a more reliable indicator of biological fitness in reality, males do not have universal preference for women with a low WHR (Yu & Shepard 1998).

Certainly, one may argue that it does not matter even if attractiveness does not indicate real biological fitness at all, as long as it has an indicating effect in people's minds such that people rate attractive individuals as more fit, as demonstrated by previous studies (e.g., Kalick et al. 1998). Although it might make sense, this reasoning at the same time would greatly corrode Maestripieri et al.'s critiques against explanations provided by economists and social psychologists. This is because the most critical evidence they cited to challenge these explanations was that in reality there is little or no evidence that attractive individuals are more productive, trustworthy, and competent, although people do exhibit an attractiveness halo, just as they perceive attractive persons as having higher biological fitness.

Second, the concept of "mating goal" is only a latent variable assumed by Maestripieri et al., and no study has directly manipulated or measured mating goals to investigate their roles in financial and prosocial biases listed by these authors. In other related research areas, although previous studies that manipulated mating goals showed that mating goals increased males' willingness to purchase conspicuous consumption items, as well as females' public helping tendency, a recent meta-analysis revealed strong evidence of either publication bias or *p*-hacking (or both; Shanks et al. 2015). Further, none of eight pre-registered studies (with a total sample of more than 1,600 participants) replicated the mating effect, and an overall meta-analysis including all of these studies concluded an effect that was indistinguishable from zero (Shanks et al. 2015). Therefore, the latent variable (i.e., mating goal) assumed by Maestripieri et al. seems like a river without headwaters or a tree without roots, given the insignificant effect even for explicit and direct manipulation of this variable.

Third, even if financial and prosocial biases in favor of attractive adults were driven by mating goals, they may not result from a functional purpose of increasing genetic quality for offspring. If so, attractiveness should have been valued more in the context of developing a long-term relationship. However, this is not the case. By contrast, both men and women value physical attractiveness very highly in the context of short-term mating (Buss 2003; Gangestad & Scheyd 2005). Further, Maestripieri et al. relied on the evolutionary explanation to predict higher biases in favor of attractive same-sex individuals for homosexuals. This seems problematic because there is no reason to assume a relationship between homosexuality and gene passing.

When it comes back to why there are financial and prosocial biases in favor of attractive adults, there should be an alternative explanation that has nothing to do with genetic continuity. As has been demonstrated, the perception of facial attractiveness is

very complex, both in the large number of traits that determine attraction and in the variety of factors that alter attraction to particular faces (Little 2014). What might be most familiar to us is that facial attractiveness is highly dependent on sociocultural factors such as mass media influence and cultural transmission (e.g., Dakanalis & Riva 2013; Kenrick & Gutierrez 1980; Little 2014). In a specific population during a specific era, people tend to share a general standard of facial attractiveness (e.g., thin face with sharp chin in modern society and fat face with thick chin in Chinese Tang Dynasty for women), which assigns value to faces in line with such standard and makes these faces valuable and rewarding. This would directly explain why some regions in the brain's rewarding system, such as the medial orbitofrontal cortex, could be activated in response to both same-sex and opposite-sex attractive faces (O'Doherty et al. 2003; Winston et al. 2007). Although there are some basic facial features determining attractiveness that seem universally accepted across cultures and times, such as symmetry, they are more likely to result from other mechanisms such as the need to recognize objects irrespective of their position and orientation in the visual word (Enquist & Arak 1994), rather than signaling genetic quality. Furthermore, for heterosexuals, because attractiveness in opposite-sex adults is related to sexual experience, which is also rewarding, it would not be surprising that other regions processing rewarding stimuli, such as the ventromedial prefrontal cortex, are activated by attractive opposite-sex faces (O'Doherty et al. 2003). Likewise, the rewarding system is also activated in response to attractive same-sex faces for homosexuals (Ishai 2007). Therefore, because of the rewarding property of attractiveness, in the labor market or economic games, attractive individuals would generally be treated better, especially when there is a potential chance for treaters who are in pursuit of a stimulating sexual experience.

It is not all about mating: Attractiveness predicts partner value across multiple relationship domains

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Abstract: An account of the “beauty premium” based only on mating motivations overlooks adaptationist models of social valuation that have broader explanatory power. We suggest a broader approach based on evolved preferences for attractive partners in multiple cooperative domains (not just mating), which accounts for many observations of attractiveness-based preferential treatment more comfortably than does the target article’s mating-specific account.

The target article argues that the preferential treatment accorded to attractive people in labor markets, economic games, the justice system, and other social domains is primarily the result of evolved mechanisms designed to maintain access to and court valuable potential mates. We applaud the authors for comprehensively reviewing the relevant literature from multiple fields and for using evolutionary theory to integrate and explain diverse findings. We hope to see more such efforts in the future.

To support their hypothesis, the authors point to evidence that the “beauty premium” occurs somewhat more strongly and

consistently toward women and in opposite-sex interactions. They conclude that the existence of these mating-specific biases is crucial for the validity of evolutionary explanations:

If future empirical studies or reviews of the literature fail to confirm that financial and prosocial biases toward attractive people are stronger in opposite-sex than in same-sex interactions, this would indicate that the evolutionary models of attractiveness-related biases are limited in their ability to account for this phenomenon in its entirety... (sect. 7, para. 3)

In our view, this position inaccurately conflates mating mechanisms with evolutionary explanations in general. Moreover, the mating-specific hypothesis put forth by Maestriepieri overlooks alternative adaptationist perspectives on partner choice that may better explain patterns of preferential treatment directed toward physically attractive individuals.

Human social life involves multiple types of long-term cooperative relationships, including trading partnerships, friendships, mating relationships, coalitions, and leader-follower hierarchies (Tooby et al. 2006), all of which involve costly investments in specific individuals with delayed payoffs. Therefore, natural selection would have favored individuals who were attracted to others with traits that ancestrally predicted positive expected returns on these social investments (e.g., Barclay 2016; Sugiyama 2015; Tooby & Cosmides 1996). For example, there would have been strong selection against investing in friends, mates, or allies who would not be alive to reciprocate later on; who could not accumulate sufficient resources to provide help during times of need; or who carried a high load of infectious pathogens.

Because certain physical characteristics may have been cues of partner value in multiple relationship domains, physical attractiveness is likely to predict favorable treatment in multiple domains. For example, physical symmetry, smooth skin, hormone-mediated sexual ornaments, and the lack of disfigurement are all ancestrally valid indicators of good health and low pathogen load (Little et al. 2011; Kurzban & Leary 2001; Sugiyama 2015). These features would therefore have predicted longevity, continued ability to extract resources from the environment, and low risk of transmitting pathogens, all of which are valuable in multiple types of social partners. Likewise, cues of physical prowess and coordination, which would have predicted human ancestors’ ability to accumulate resources via effective foraging (Apicella 2014) and social bargaining (Sell et al. 2009), should also be attractive in multiple types of social partners. Therefore, to the degree that cues of (ancestral) mate value overlap with cues of (ancestral) partner value in other domains, mate attractiveness should predict favorable treatment in a variety of settings.

This broader partner choice-based approach predicts that people will direct preferential treatment toward attractive others as an investment in a cooperative relationship, and that this will often be true for both sexes, within same- and opposite-sex relationships, and also among people of nonreproductive ages. Evidence is overwhelmingly consistent with these predictions. For example, the meta-analytic review by Langlois et al. (2000) showed that attractive males and females receive preferential treatment within children’s peer groups, adult-child dyads, and interactions among both same- and opposite-sex adults. Many researchers have found correlations between physically attractive features and social connectedness, status, and income within both same- and mixed-sex organizations (e.g., Anderson et al. 2001; Judge & Cable 2004; Little & Roberts 2012; Tyrrell et al. 2016). We recently found that men playing the ultimatum game were more generous to *other men* who appeared healthier, more attractive, and physically stronger, and that this latter effect was attributable to strength triggering perceptions of productivity rather than intimidation (Eisenbruch et al., in press). Physical attractiveness alone predicted nearly two-thirds of the variance in how generously men were treated by other men. Similarly, we recently showed that both men and women willingly allocate positions of high organizational status and income to physically stronger (and

hence more attractive) men, because they are seen as being better able to enforce cooperation within the group and successfully negotiate with other groups (Lukaszewski et al. 2016). These effects are incongruous with the target article's mating-specific account, but are consistent with an evolved psychology of partner choice in which mate choice shares desiderata with partner choice in other social domains.

We emphasize that we agree with the argument made by Maestriperi et al. that mating motivations likely explain any tendency for attractiveness-based preferential treatment to be strongest from men toward women. Mating is highly fitness relevant, and it is therefore likely that mating motives have particularly powerful effects on (especially men's) behavior. We reject, however, the idea that these sex effects should be the litmus test for evolutionary explanations of the "beauty premium," or that attractiveness effects in nonmating domains must be the result of overgeneralizations of mate choice mechanisms. In addition, we are not arguing that attractive individuals are necessarily better cooperative partners in contemporary environments; rather, physical attractiveness in cooperative partners likely predicted larger streams of material benefits within ancestral hunter-gatherer environments, even if it does not reliably predict worker performance in technologically modern occupations. Because partner choice mechanisms evolved in such ancestral ecologies, those mechanisms may still produce preferences for attractive cooperative partners in modern economies. Whether attractive individuals continue to be differentially productive within at least some modern organizations, for example, by virtue of their ability to elicit prosocial behavior in customers, clients, or other workers, is an important empirical question for future research.

In sum, because mate choice is not the only type of partner choice that has benefited from preferences for physical attractiveness, any account that depends exclusively on mate choice to explain broad preferences for attractive people will likely be incomplete.

The type of behavior and the role of relationship length in mate choice for prosociality among physically attractive individuals

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Abstract: Two further key aspects of prosociality as a sexual signal are explored here. First, the context in which it is used (in particular, relationship length) and, second, the different types of prosocial behaviors that exist in social interactions. Therefore, this commentary can show why prosocial behaviors are biased toward physically attractive individuals, as they can gain valuable information from them.

The role of prosocial behaviors as courtship displays has received a great deal of attention (e.g., Farrelly et al. 2007; Iredale et al. 2008; Miller 2000; Phillips et al. 2008). As such, it has contributed greatly to our understanding of why humans behave altruistically from a Darwinian perspective. That the target article not only recognizes this, but also suggests from the body of evidence that mating motives are a key cause of prosocial biases to attractive individuals is pleasing to see, and I agree fully. However, I believe that the target article curtailed its investigation of this too early, and a more interesting and revealing understanding can be gleaned when one goes further. This commentary aims to do just that, by focusing on the *contexts* in which prosocial

biases are used in mate choice as courtship displays (as suggested in the conclusion of the target article) and also, importantly, on the different *types* of prosocial behavior that exist. As part of this, it is essential to not just concentrate on research findings of actual prosocial behaviors, which the target article has done comprehensively. Instead, this commentary will also discuss research that shows the counterpart to this, if indeed a key cause is mating motives; namely, what is it about prosocial behaviors that all individuals (including, of course, physically attractive ones) find desirable in mate choice?

A particularly important context to consider is the role of length of relationship. Here there is very strong experimental support for prosocial behaviors being more desirable for longer relationships (Barclay 2010; Farrelly 2011; 2013; Farrelly et al. 2016; Guo et al. 2015; Moore et al. 2013; Oda et al. 2014), as well as having an important role cross-culturally in actual long-term relationships (Stavrova & Ehlebracht 2015; Tognetti et al. 2014). This suggests that prosocial behavior is signaling good phenotypic quality, that is, the ability of the signaler to provide and support as a good partner or parent (Farrelly 2011; Kokko 1998; Miller 2007). Furthermore, the lack of preferences for prosocial males for short-term relationships among females at the fertile stage of their menstrual cycle (Farrelly 2011; Oda et al. 2014), as well as *non*-prosocial men being preferred by women for short-term relationships (Farrelly et al. 2016), suggests that an alternative signal, that of good genetic quality (Miller 2000), cannot account for mate choice preferences for prosocial behavior. Therefore, these findings offer support for the sexual-signaling hypothesis of the target article because, as the authors highlight, it suggests that prosocial behaviors are signaling desirable mate choice traits. More importantly, however, the role of relationship length makes an important contribution as we are now able to surmise more precisely *what* is being signaled.

Additionally, more can be revealed about the target article's aims if we consider that there exist a myriad of types of behaviors that can be considered "prosocial." Once this is recognized, a more in-depth investigation of the role of such behaviors in mate choice can be revealing. For example, from the research in the target article that looks at economic games, it is suggested that the parameters of different games mean different types of prosocial behaviors are being signaled. Although, as the target article recognizes, different games tend to produce similar findings with regard to the effects of physical attractiveness, this is not always the case. For example, Jensen (2013) found no increased prosociality to attractive opposite-sex individuals with the trust game. This raises a particularly interesting question: Can behavior signaled in this game, *trustworthiness*, be considered clearly distinctive from that of other games such as the dictator or ultimatum game, which can perhaps be associated with generosity, or the prisoner's dilemma game, which is often considered a measure of reciprocal cooperation? In a similar vein, *fairness* in a particular interaction, rather than indiscriminate prosociality (i.e., helping anyone), will be interpreted differently, so is there a difference in individuals' biases to display these to physically attractive observers? Little research exists to answer this, but a recent study found that behaving fairly occurred more than overall prosociality toward physically attractive partners in an ultimatum game (Bhagal et al. 2016). Elsewhere, Guo et al. (2015) found that a cultural norm among Chinese undergraduates had a great influence over the role of kin altruism, making this type of prosocial behavior unusual in mate choice as it was preferred more by men (and signaled more by women). Finally, heroism can be considered an additional category of prosocial behavior, which, although it too has been shown to be an important trait in mate choice (Farthing 2005; 2007; Kelly & Dunbar 2001) and therefore more likely to be biased toward attractive individuals, is unfortunately not addressed in the target article. Overall this is not to say that the premise of the target article and the body of research is flawed, as the majority of prosocial behaviors researched do indeed show their value in mate choice

scenarios, suggesting that they signal a similar value. However, a more nuanced and careful view of what “prosocial behavior” may constitute in future research that examines such biases toward attractive individuals is clearly warranted.

To conclude, the aims of this commentary were not only to support the argument of the target article that evolutionary explanations can best account for biases in prosocial behavior toward physically attractive individuals, but also to build on this further with a more detailed analysis of research into the role of such behaviors in mate choice. The analysis of the latter aim suggests that one should expect such biases to be more prominent in mating contexts where individuals may be seeking more long-term, committed relationships (perhaps the modern workplace, which the target article does show often happens) and also pay attention to what aspect of “prosociality” the biases are signaling, to enlighten us and further aid our understanding.

Understanding the physical attractiveness literature: Qualitative reviews versus meta-analysis

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Abstract: The target article is a qualitative review of selected findings in the physical attractiveness literature. This commentary explains why the meta-analytic approach, frequently used by other attractiveness reviewers, is preferable for drawing unbiased conclusions about the effects of attractiveness. The article’s main contribution is affording a foundation for subsequent meta-analysis of the studies discussed in a subjective fashion.

The identification of the physical attractiveness stereotype—initially encapsulated as “what is beautiful is good” (Dion et al. 1972)—and a seminal qualitative review of the then emerging physical attractiveness literature (Berscheid & Walster 1974) engendered a tsunami of multidisciplinary research on physical appearance over the past four decades. Unsurprisingly, meta-analysis has been commonly used to review findings from the thousands of studies of physical attractiveness. Meta-analyses have examined the attractiveness stereotype (Eagly et al. 1991; Feingold 1992a), correlations between attractiveness and other characteristics (Feingold 1992a; Jackson et al. 1995; Langlois et al. 2000), and the effects of attractiveness on decision making in mate selection (Feingold 1988; 1990), employment (Hosoda et al. 2003), and the courtroom (Mazzella & Feingold 1994).

In these meta-analyses, many of which were cited in the target article, investigators began by specifying methods for study retrieval (e.g., databases searched) and study inclusion criteria. Although these steps should be taken for narrative (qualitative) and for meta-analytic reviews, they were rarely used for the former until their importance was highlighted by pioneering meta-analysts critical of traditional reviews. In addition, meta-analyses focus on effect sizes (including moderators of effect sizes) and their confidence intervals for findings, rather than on null hypothesis significance tests. The former approach is now widely recognized as preferable and is supplanting the latter, even in empirical research (Cumming 2013; Feingold 2015).

The target article is an old-school qualitative review in the mold of Berscheid and Walster (1974). The authors do not provide the criteria used to locate or include studies for their review, although one evident criterion for inclusion was that a study had to have found a positive effect of physical attractiveness on social treatment. However, when a meta-analysis found an overall effect of

attractiveness to be nonsignificant, there were often empirical studies included in that review that had found significant effects. Hence, with a narrative review approach that allows for cherry picking of studies based on statistical significance (and capitalizing on type I errors) to be cited, physical attractiveness effects may appear to be more pervasive and robust than they actually are. Consequently, researchers who conduct qualitative reviews of the attractiveness literature may draw tendentious conclusions that are inconsistent with findings from past or future meta-analyses conducted with a comprehensive and objectively selected set of studies and addressing issues with publication bias, outliers, and among-study variations in effects.

The discussion in the target article (and its abstract) adheres to the classical view of the physical attractiveness stereotype, that is, that all desirable attributes are more likely to be ascribed to the attractive than to the unattractive, and ignores moderation of attractiveness effects by type of attribute. The review also concluded that the stereotype is strongest for perceptions of women and of the opposite sex. But are these broad conclusions supported by meta-analyses of the attractiveness stereotyping literature?

Two independent meta-analyses that have synthesized findings from experiments on the physical attractiveness stereotype (Eagly et al. 1991; Feingold 1992a) suggest otherwise. Feingold (1992a) found observers were most likely to attribute social skills and extraversion (sociability and dominance) to physically attractive targets. The attractive were seen as only moderately more mentally healthy and intelligent. Most important, given the frequent use of the term “good” to describe perceptions of the attractive, this meta-analysis found that attributions of character (e.g., honesty and trustworthiness) were unaffected by target attractiveness, and the attractive were viewed as less modest (e.g., vainer). The moderation of effect sizes by target gender was also examined, and no significant differences on attributions of social competence, intelligence, and personality traits were found. Most important, Target Gender \times Target Attractiveness \times Participant Gender interactions were all nonsignificant.

Eagly et al. (1991) also examined the moderation of effects of attractiveness by attribute. The abstract of their meta-analysis noted, “The differences in subjects’ perception of attractive and unattractive targets were largest for indexes of social competence; intermediate for potency, adjustment, and intellectual competence; and near zero for integrity and concern for others” (p. 109), which is consistent with the findings from Feingold (1992a). The Eagly et al. meta-analysis also found no significant differences in effect sizes between male and female targets for the different attributes examined, which was also in accord with Feingold (1992a). However, the findings from the meta-analyses are inconsistent with the conclusion of the target article that the physical attractiveness stereotype is more potent in perceptions of women than of men, and for opposite-sex rather than same-sex evaluations.

The target article also cited Mazzella and Feingold’s (1994) meta-analysis on the effects of defendants’ physical attractiveness on sentencing recommendations by mock jurors as affording more evidence for the ubiquitous benefits of physical attractiveness, although averring that the attractiveness advantage was greater for perpetrators of some crimes than for others. Although the meta-analysis did indeed find a positive effect of target attractiveness on punishment recommendations, the mean effect size (d) of 0.12 was trivial, and the Defendant Attractiveness \times Crime interaction was misinterpreted as ordinal. Although physical attractiveness was beneficial to defendants guilty of theft, rape, or cheating, no effect of attractiveness was found for swindling, and attractive defendants were treated more punitively than unattractive defendants for negligent homicide. (The strong crossover interaction explained the weak main effect of attractiveness captured by the mean effect size from all studies.) Hence, the right interpretation of the meta-analytic results is that physical attractiveness may or may not affect sentencing recommendations for

defendants depending on the nature of crime, and its effects may be positive or negative.

The main contribution of the target article is in providing a conceptual model that affords a foundation for a subsequent meta-analysis of findings of attractiveness effects discussed that were not synthesized in earlier quantitative reviews, much as Berscheid and Walster (1974) paved the way for past meta-analyses of attractiveness effects from older work. Such a research synthesis of new domains should address moderators of attractiveness effects besides gender, and their associated effect sizes and confidence intervals.

Mating motives are neither necessary nor sufficient to create the beauty premium

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Abstract: Mating motives lead decision makers to favor attractive people, but this favoritism is not sufficient to create a beauty premium in competitive settings. Further, economic approaches to discrimination, when correctly characterized, could neatly accommodate the experimental and field evidence of a beauty premium. Connecting labor economics and evolutionary psychology is laudable, but mating motives do not explain the beauty premium.

Maestripieri et al. review large literatures on the beauty premium and consider theories that cross disciplinary boundaries, including their preferred perspective of evolutionary psychology. That effort is commendable, and connecting literatures could lead to useful research cross-pollination and new possibilities for policy makers to combat discrimination. We agree that mating motives play a role in decisions that favor attractive individuals. Mating motives alone, however, are neither sufficient to explain the persistence of these biases in key environments like the labor market nor necessary for these biases to occur in the first place. In the former case, Maestripieri et al. ironically fail to consider what hiring strategies are most fit in a competitive environment. In the latter case, they mischaracterize economic approaches to discrimination that can explain the beauty premium in the absence of mating motives (and also explain why humans prefer attractiveness).

1. Mating motives cannot explain discrimination in labor markets. Maestripieri et al. attempt to explain the beauty premium in labor markets by recourse to the behavior of individual decision makers. For example, they note that “when a male employer has the opportunity to hire an attractive female employee ... it is likely that the man’s mating motivation is activated” (sect. 5.2.1, para. 5). But if attractive females are not more productive workers, as the authors’ review suggests, then an arbitrage opportunity is available for any firm that does not have this bias: More productive workers will be available at lower prices. Even if this advantage is small, over time arbitrageurs will win and biased firms will lose, similar to how functional adaptations survive in species, and a small number of unbiased firms can wipe out the beauty premium. Theories of why individuals share resources with attractive people are hence not sufficient to explain the beauty premium in labor markets. Our next and perhaps most crucial point explains why they are not a necessary explanation.

2. (At least) two flavors of discrimination. Maestripieri et al. criticize economic models of discrimination for not explaining why attractiveness is favored. In favor of mating motives, they provide a mechanism behind attractiveness preferences in mating that is putatively non-economic (sect. 2.1.3, para. 2): “In fact, human facial attractiveness is likely to be an indicator of

overall quality, including greater genetic quality, lower exposure to stress during early development, greater resistance to diseases and parasites, and greater fertility.” This argument essentially states that because genetic quality cannot be directly observed, people use attractiveness as a proxy for quality, and on average, they are better off than if they ignored this useful information.

The idea that attractiveness is correlated with desirable but unobserved qualities, however, coincides exactly with the economic concept of *statistical discrimination* (Arrow 1973). Like mating partners, employers also want to identify positive qualities, particularly productivity, that they cannot directly or perfectly observe. Hence, the preference for observables like attractiveness can be explained as identifying groups that have higher average productivity. We are puzzled how it can be fit to judge that attractive people have greater genetic quality and health (according to Maestripieri et al. themselves), yet not fit to judge that they are likely better or more reliable workers. It is not necessary that the hiring individual wants proximity to sexually attractive people for the beauty premium to occur; if attractiveness is a cue to mate quality, it is often a cue to worker quality. Although economists tend to assume that in equilibrium, such discrimination is rational, they need not even be correct in their beliefs that attractive workers are, on average, better for statistical discrimination to operate.

For example, Maestripieri et al. discuss the experiment by Mobius and Rosenblat (2006), in which attractive workers were paid more even when they only had phone interviews with their experimental employers. Mobius and Rosenblat interpret this result as reflecting statistical discrimination; more attractive people were more confident, which was used as a proxy to judge their productivity. Attractive workers were not more productive, a fact that Maestripieri et al. note in this and several other experiments, but that does not mean that the statistical rule of favoring attractive or confident people is generally useless. As evolutionary psychologists and others have noted, otherwise adaptive heuristics often fail to apply in one-off experimental settings (e.g., Gigerenzer et al. 1991).

Maestripieri et al. omit the concept of statistical discrimination and treat taste-based discrimination—a premium given to members of a group even if productivity were observable (Becker 1957)—as the only economic approach, despite several recent studies that distinguish taste-based from statistical in lab experiments (Mobius & Rosenblat 2006), field experiments (List 2004), and archival real-world data (Abrams et al. 2012; Price & Wolfers 2010). These distinctions are important for understanding the cause of discriminatory outcomes, and neither can explain all instances of discrimination. When hiring a waitress at a Hooters restaurant or an actor for a Hollywood movie, taste-based discrimination on attractiveness may occur. But is it more likely that attractive actors are hired because the producer wants proximity to them for sexual reasons or because audiences who will never be close to them like seeing beautiful people in movies? Even in our examples, the source of taste-based discrimination is plausibly customers, and a profit-minded firm would hire for beauty regardless of the hiring agent’s sexual tastes.

3. Integration instead of either-or questions. Mating motives cannot supplant all other explanations of the beauty premium. But instead of asking whether discrimination is better explained by *either* economic theories *or* psychological theories, we believe the most progress comes from integrating the two approaches. The taste-based versus statistical distinction could be useful to psychologists who study discrimination or mating preferences. Evolutionary psychology could provide labor economists with a more nuanced and molecular understanding of the origins of statistical beliefs that attractive workers are more productive. Similarly, the idea of mating motives could shed light on the nature of taste-based desires to affiliate with attractive people that ultimately lead to discrimination. The impact on research and policy is greatest when these multiple mechanisms are considered in concert.

Oxytocin drives prosocial biases in favor of attractive people

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Abstract: Current perspectives on attractiveness-related prosocial biases emphasize the contribution of evolutionarily shaped mating drives. Here, we extend these concepts by highlighting the pivotal role of the hypothalamic peptide oxytocin in augmenting the salience and rewarding value of social stimuli, including the partner's face, thereby fostering social bonding in general and the stability of monogamous pair bonds and offspring care in particular.

The hypothalamic peptide oxytocin (OT) is a member of the ancient class of nonapeptides, conserved throughout evolution from nematodes to humans (Donaldson & Young 2008). OT controls lactation and parturition, and in the brain it influences social cognitive functions and a diverse repertoire of social behaviors, ranging from pair-bond formation to mating and parenting (Insel 2010; Insel & Young 2001; Rilling & Young 2014). Consistent with this profile, the OT receptors are enriched in a widely distributed network of brain regions engaged in social and cognitive plasticity (Mitre et al. 2016).

The central role of OT in pair bonding has been revealed in various species, including zebra finches (Klatt & Goodson 2013) and teleost fish (Oldfield & Hofmann 2011), and is particularly evident in comparisons between the monogamous prairie vole and the polygamous montane vole (Carter 1998; Young & Wang 2004). In contrast to the latter, prairie voles exhibit a high density of OT receptors in the prelimbic cortex and nucleus accumbens (NAcc), which receive dense inputs from other signaling pathways, including dopamine (DA) and arginine-vasopressin, to facilitate monogamous behavior (Johnson & Young 2015).

Findings linking OT to infant-caregiver bonding (Hurlmann & Scheele 2016) encompass increased peripheral OT levels during parent-child interactions, on the one hand, (Feldman et al. 2010) and variations in the OT receptor gene that relate to differences in parenting sensitivity, on the other (Feldman et al. 2012). Because it is still unclear whether peripheral levels of OT predict central levels (Carson et al. 2015; Landgraf & Neumann 2004), stronger evidence for a key role of OT in infant-caregiver bonding comes from experimental studies relying on exogenous administration of OT, usually realized through nasal delivery of the peptide (Quintana et al. 2016; Striepens et al. 2013). Exogenously administered OT augments affective parenting (Weisman et al. 2012) and modulates fathers' neural responses to pictures of their own children (Wittfoth-Schardt et al. 2012). Furthermore, OT promotes relationship stability by stimulating positive communication during couple conflict (Ditzen et al. 2009) and by increasing trust following betrayal (Baumgartner et al. 2008). Although these subtle, modulatory effects of OT are influenced by a panoply of person-dependent factors including sex (Scheele et al. 2014b), personality (Scheele et al. 2014a), and early life adversity (Meinlschmidt & Heim 2007), they clearly support the highly adaptive role of the peptide in the formation and maintenance of social bonds.

In their superb article, Maestriperi et al. focus on attractiveness-related prosocial biases that occur when adults interact with one another. Endogenous OT is increasingly released during experiences of romantic love (Schneiderman et al. 2012), social support

(Grewen et al. 2005), and generosity (Zak et al. 2005). Studies relying on exogenous OT administration have shown that the peptide modulates a wide range of prosocial and courtship behaviors in humans, including interpersonal distance in people engaged in monogamous relationships (Preckel et al. 2014; Scheele et al. 2012), altruism (Hu et al. 2016; Marsh et al. 2015), trust (Kosfeld et al. 2005), generosity (Zak et al. 2007), and empathy (Domes et al. 2007; Hurlmann et al. 2010; Radke & de Bruijn 2015). As Maestriperi et al. point out, several of these behavioral changes affect the perceived attractiveness of a person as a potential mating partner. As a direct confirmation of this proposition, a recent study confirmed that perceived attractiveness of a person depends on that person's affective behavior (Anders et al. 2016).

The behavioral effects of OT may result from perceptual changes, including increased attention to the socially informative eye region (Guastella et al. 2008), improved recognition of cues related to sex and relationship (Unkelbach et al. 2008), and facilitated sensing of and responding to emotional stimuli (Shahrestani et al. 2013). Of particular relevance to the emergence of attractiveness-related biases are observations that OT increases ratings of trustworthiness and attractiveness of male and female targets in judgments of both sexes (Theodoridou et al. 2009, but see also Lambert et al. 2014; Thienel et al. 2014). Noteworthy is that OT also improves men's ratings of the likeability of physically formidable male peers (Chen et al. 2015), clearly showing that OT-mediated attractiveness biases are not restricted to individuals of the opposite sex. In addition, OT enhances an attractiveness bias for the romantic partner (Scheele et al. 2013; 2016), and this behavioral effect is accompanied by enhanced responses in reward-associated brain areas including the ventral tegmental area and the NAcc, with the latter being rich in OT-DA d2 receptor heteromers (Romero-Fernandez et al. 2013). However, a positron emission tomography study employing the DA d2 receptor radioligand [¹¹C]raclopride and a facial attractiveness rating task failed to detect altered striatal DA release as a correlate of an OT-mediated attractiveness bias (Striepens et al. 2014). Instead, there is growing evidence from rodent studies for OT interactions with the serotonin system (5-HT) in the NAcc during encoding of social reward (Dölen et al. 2013; see also Mottolese et al. 2014). Hence, OT-mediated attractiveness biases may be anchored in interactions of the peptide with diverse signaling pathways, including 5-HT, but also gonadal steroids such as testosterone, as mentioned by Maestriperi et al. Interestingly, OT stimulates testosterone release (Frayne & Nicholson 1995; Gossen et al. 2012; Weisman et al. 2014, but see also Wirth et al. 2015), heightened OT levels co-occur with elevated testosterone levels (Jaeggi et al. 2015), and prenatal exposure to testosterone moderates later OT effects (Kret & De Dreu 2013; Weisman et al. 2015).

In quintessence, OT has a key role in modulating social cognition and behavior, with the ultimate aim to foster social bonding in general and the stability of monogamous pair bonds and offspring care in particular. Given this empirical background, we propose that the attractiveness-related prosocial biases described by Maestriperi et al. may very likely be orchestrated by, and depend on, OT signaling and represent a relic of our evolutionary past.

Omitted evidence undermines sexual motives explanation for attractiveness bias

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Abstract: This commentary makes three points: (1) the existing evidence does not consistently favor the proposed sex difference in attractiveness preferences, nor the fitness-related outcomes of attractiveness; (2) the neglected association of perceived attractiveness and trustworthiness allowed the authors to incorrectly attribute many findings solely to attractiveness, and (3) the importance accorded attractiveness in mate preferences is culturally shaped and likely evolutionarily novel.

Maestriepieri et al. appear to be unaware of important advances in understanding the role of attractiveness in mate preferences and relationship outcomes. In the context of relationships, evidence does not support the claim that a partner's physical attractiveness is more valued by men than women. Specifically, the meta-analysis of 95 articles by Eastwick et al. (2014a) showed that physical attractiveness predicted romantic attraction very similarly for men ($r=0.43$) and women ($r=0.40$); see also the critique by Meltzer et al. (2014) and the rejoinder by Eastwick et al. (2014b). For example, Selterman et al. (2015) found that participants in a speed-dating study were more interested in potential partners who were attractive and good potential earners, with neither preference moderated by gender. However, the greater valuing of attractiveness by men than women is robust in assessments of preferences for ideal hypothetical partners (e.g., Feingold 1992b), a context far less relevant to fitness outcomes than actual relationships.

Also weak is evidence that attractiveness is an honest signal of health and reproductive success. Reviews have found attractiveness and related facial characteristics weakly or inconsistently linked to actual health (Henderson et al. 2016; Weeden & Sabini 2005). In addition, Weeden and Sabini (2005) found women's health was related not to facial attractiveness, but to waist-to-hip ratio and weight. Yet, most researchers cited by Maestriepieri et al. operationalized attractiveness by head or head-and-shoulders photos varying in facial attractiveness.

Even more critical to the sexual motives argument of Maestriepieri et al. would be evidence that attractiveness serves as an honest signal of fertility. This prediction is best examined in populations with low contraceptive use. A study in rural Senegal, where there is little access to modern birth control, found that facial attractiveness negatively predicted age-specific reproduction in both sexes (Silva et al. 2012). These investigators also found a negative relation of facial attractiveness to lifetime reproductive success among men who graduated from the West Point Military Academy in 1950. Earlier studies relating attractiveness to reproductive outcomes have produced inconsistent findings (see Silva et al. 2012). For example, in a large U.S. sample, attractiveness showed only a weak positive relation to reproductive success in women and men, once marriage was taken into account (Jokela 2009). In general, evidence that fitness gains would follow from attractiveness preferences is weak and inconsistent.

The authors also neglected the relation between attractiveness and trustworthiness, thereby underestimating trustworthiness's impact. Considerable evidence shows that attractive people are trusted more than unattractive people (e.g., Kaisler & Leder 2016; Palmer & Peterson 2016). However, trustworthiness is not merely one of several positive traits associated with perceived attractiveness, but is a central trait revealed directly from physical appearance. In addition to attractiveness, faces are informative about two other evolutionarily adaptive attributes – namely, trustworthiness and dominance (Oosterhof & Todorov 2008). Research has thus shown that three core dimensions describe the information directly available from faces: trustworthiness, dominance, and youthful attractiveness (Sutherland et al. 2013).

In some studies, trustworthiness has actually trumped attractiveness in affecting positive outcomes. For example, in a peer-to-peer lending study, Duarte et al. (2012) found little effect of borrowers' perceived attractiveness but a benefit of their perceived trustworthiness. A similar result emerged in an economic game study where perceived trustworthiness, but not attractiveness, predicted the amount of money sent to the partner (van't Wout & Sanfey 2008). In other contexts, trustworthiness and attractiveness sometimes show high levels of shared variance (Ohanian 1991; Sofer et al.

2015). Indeed, a meta-analysis found that attractiveness and trustworthiness are subserved by overlapping brain networks (Bzdok et al. 2011). Finally, an investigation of the relation between facial trustworthiness and attractiveness in children and adults concluded that facial attractiveness might have heuristic value in signaling trustworthiness and thus guiding decision making (Ma et al. 2015). In sum, by focusing on one aspect of face perception, namely, attractiveness, and contending that trustworthiness is merely stereotypically associated with attractiveness, the authors have ignored the feature that arguably has more adaptive significance and predictive validity.

Concerning cultural variation, preferences for attractive partners may be largely a modern phenomenon, not a pattern typical of early humans. Consider that most human evolution took place in simple band societies, characterized by small, dispersed living groups of cooperating families (Gintis et al. 2015). Given that cultures have rules that restrict marriage options, people in band societies typically would have obtained mates from few possibilities. Moreover, people would not have been exposed to many exemplars of opposite-sex persons differing in the physical attributes that are correlated with attractiveness in WEIRD (Western, educated, industrialized, rich, democratic) cultures (Henrich et al. 2010). With industrialization and urbanization, massive direct and indirect exposure to large numbers of people favors learning the nuances of attractiveness. From this perspective, research by Scott et al. (2014) on preferences for opposite-sex faces is valuable because data were obtained from 12 populations differing greatly in economic development. The expected preferences for faces with sexually dimorphic features, that is, of men for feminine faces and of women for masculine faces, increased in urbanized and developed societies. These features signal attractiveness much more in contexts of exposure to large amounts of visual information about faces.

Fostered by massive media exposure, consensual cultural norms develop about what constitutes attractiveness. For example, norms about female attractiveness vary between black and white populations in the United States, with thin bodies considered attractive among whites, but attractiveness among blacks extending to heavier women (Chithambo & Huey 2013). In general, standards about what attributes of bodies and faces are attractive show considerable cultural shaping, whereas cues to ugliness show more cross-cultural consensus (Sorokowski et al. 2014). As Zebrowitz and Rhodes (2004) found, attractiveness was validly associated with health and intelligence only in a sample of persons judged below-average in attractiveness. If so, avoiding unattractive mates may have evolutionary roots because ugliness can be an honest signal for poor health and infertility. Preference for attractive mates, with attractiveness signaled by certain facial and bodily features, is more likely governed primarily by sociocultural processes.

On completion of this commentary, we were astonished that the overlap of citations between the target article and our commentary consists only of two articles (van't Wout & Sanfey 2008; Zebrowitz & Rhodes 2004). This omission of key evidence that counters the thesis of the target article illustrates the principle of attitudinal selective exposure to information (see meta-analysis by Hart et al. 2009): Unless accuracy is a clear goal, people tend to seek out and consume information congenial to their pre-existing preferences. Scientists, in particular, often find it difficult to overcome fixing on research findings based on their compatibility with their preferred theory.

The out-of-my-league effect

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Abstract: When taking into account the chances of success, strategic mating motivations do imply a bias not toward the most attractive individuals, but toward average or mildly attractive individuals, undermining the explanation of Maestriepieri et al. at a fundamental level. This leaves open the possibility of alternative explanations and calls for a full-fledged explicit model of courtship behavior.

To explain financial and prosocial biases toward attractive adults, Maestriepieri et al. defend a “strategic mating behavior” account. Their central argument relies on a causal relationship between viewing attractive individuals (A); a host of cognitive, emotional, and physiological changes (B); and financial/social generosity or other desirable behaviors (C). Yet, their reasoning is based on data from a collection of different experimental studies, and one cannot reliably determine how much (if any) of the effect of A (e.g., attractiveness) on C (e.g., financial decision) is actually explained by B (e.g., testosterone). Their review therefore provides no definitive evidence that mating motives or their proxies (e.g., physiological changes) are the actual *causes* of an attractiveness bias. There are in fact theoretical reasons to doubt the accuracy of a causal effect. This comment will focus on the idea that strategic mating behavior does not generally imply that favors should increase with attractiveness: a phenomenon we label the *out-of-my-league effect*.

The target article’s argumentation is grounded on a mating model in which only the benefits of mating with attractive people are considered. This completely overlooks the effect of the probability of success in mating: A simple model of courtship behavior should take into account not only the benefit of mating with an attractive individual, but also the probability of doing so—itsself determined by the mating opportunities of others. The potential “court maker,” if motivated solely by mating per se as hypothesized, faces a trade-off between the benefit of mating and the probability of success: Whereas the former increases, the latter realistically decreases with the attractiveness of the target. For a given attractiveness of the court maker, attractiveness-based matching implies that the probability of success decreases with the attractiveness of the potential mate, as the target’s opportunities are likewise based on attractiveness. If the probability of success decreases more steeply than the benefit of mating increases given the potential mate’s attractiveness, then the more attractive the potential mate, the lower is the expected benefit of a match, that is, the benefit of a match weighted by its probability of occurrence. The out-of-my-league hypothesis states that one should not spend resources to court a very attractive potential mate with a minimal probability of success, but rather prefer a moderately attractive one with a reasonable chance of success. In a nutshell: To mate or not to mate is not the question, but rather with whom.

In fact, at the population level, “smart” courtship behavior is more likely to lead, on average, to a bias toward average-looking individuals: If the distribution of attractiveness is concentrated around its mean (such as in a normal distribution, for example), individuals will most likely favor moderately rather than highly attractive

mates. In terms of strategy, the average court-making agent is better off targeting individuals of intermediate attractiveness. Not only is it the rational strategy, but also it is the fittest one from an evolutionary standpoint: An individual systematically favoring much more attractive individuals than herself is less likely to mate, and this behavioral pattern is more likely to disappear from the population by evolutionary pressure. This explains the opportunity costs associated with trying to mate with very attractive individuals, which is largely excluded from the analysis by Maestriepieri et al.

In other words, there is no guarantee that the relationship between the level of effort by the courter will be monotonic with the attractiveness of the potential mate; quite the reverse may occur, because positive assortative matching implies that “birds of a feather flock together” (McPherson et al. 2001). The courtship explanation, implicitly based on an endogenous matching model, thus has implications at odds with the set of empirical facts it aims to explain. A complete model of endogenous mating is needed to understand the evolutionary explanation. Such a model has to account not only for the effect of attractiveness on individuals’ decision making (as does the target article), but also for the general equilibrium implications of such mating behaviors that are distortions in the probability that mating is actually achieved given the relative attractiveness of the partners.

Because mating motives do not necessarily explain the attractiveness bias, it appears premature to reject economic and social psychological explanations. Indeed, the main argument for favoring a mating-based over a stereotype-based account relies on a gender moderation of the attractiveness bias. However, such moderation can be easily explained, for example, from a social psychological perspective. The *opposite-sex* beauty premium effect could simply reflect stereotypic processes. Although the authors reject these based on the fact that an attractiveness bias occurs even when controlling for personality traits and independently from stereotype-induced expectations, the stereotype content must be distinguished from its accuracy and actualization in reality (Judd & Park 1993). Furthermore, as stereotypes operate most of the time on an unconscious level and their influence cannot be captured through explicit self-reports, the reviewed evidence is not a valid rebuttal of a stereotype-based explanation. Moreover, the *same-sex* negative bias could reflect self-threat because of comparisons and/or competition with attractive individuals. A possible self-threat regulation strategy (among others) relies on derogation and destructive behaviors toward attractive individuals. Such counterproductive responses to threatening comparisons occur routinely in the workplace (Lam et al. 2011). To protect their work environment from negative comparisons, individuals can even provide poor hiring recommendations (Garcia et al. 2010). Crucially, the attractiveness gender bias appears only for individuals who are sensitive to negative comparisons, whereas the rest show a gender-independent attractiveness bias (Agthe et al. 2014).

Although the “strategic mating behavior” account in the target article is scientifically attractive, we shed light on a theoretical argument that goes against their preferred explanation. As the out-of-my-league demonstration suggests: “One’s man meat is another man’s poison.”

Context matters for attractiveness bias

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Abstract: To fully understand the attractiveness bias, we propose that contextual factors or affordances should be integrated into the mating-based evolutionary account of Maestriepieri et al. We review examples highlighting the role of contextual factors in the perception of attractiveness and in attractiveness bias. These suggest contextual factors differentially afford the development of preference for attractive others into observed habits of mind.

Maestriepieri et al. review literature on positive bias toward attractive targets and present evidence for a mating-based evolutionary account of this bias. Specifically, they propose that positive bias toward attractive targets does not reflect specific stereotypes about beauty, but instead evolved from the tendency to use attractiveness as a criterion for mate selection. Their account emphasizes evolved individual predispositions as a primary cause for the bias, but neglects the role of contextual factors. Here we argue that a full understanding of the attractiveness bias requires attention to contextual factors or affordances. Below, we provide a few examples to highlight the role of such factors in the perception of attractiveness and in attractiveness bias.

First, contextual factors such as relationship status and sex ratio affect the perception of attractiveness. Indeed, studies have shown that participants who are in a committed relationship derogate the attractiveness of opposite-sex others (Meyer et al. 2011) or even reduce attention to them (Maner et al. 2007b; Miller et al. 2012), compared with those who are single. Likewise, research has shown that attractiveness ratings are recalibrated as a function of contextual cues signaling the sex ratio in one's environment, such that symmetrical faces are rated as more attractive for the majority sex and less attractive for the minority sex (Watkins et al. 2012).

A related line of research involves subjecting people to various contextual cues and examining how this exposure affects their perceptions of attractiveness. For example, Ariely and Loewenstein (2006) exposed participants to sexually arousing cues, which led men to perceive relatively less appealing women as more attractive.

Second, there is ample evidence showing that ecological factors moderate the attractiveness bias. For example, the *pathogen-prevalence hypothesis* states that high pathogen load increases the relative importance of genetic quality and parental investment on offspring survival, accentuating preferences for mate characteristics associated with immunocompetence (e.g., physical attractiveness). In line with this proposition, research suggests that people in countries with a higher prevalence of pathogens (Gangestad & Buss 1993) or individuals who are more vulnerable to contagious diseases (DeBruine et al. 2010) value physical attractiveness in mates more than people in areas with lower prevalence or who are less vulnerable to disease. Causal evidence for this hypothesis comes from studies that manipulate pathogen threat. In these studies, people primed with pathogen prevalence preferred higher attractiveness features in potential mates as compared with participants in a control group (e.g., facial symmetry; Lee & Zietsch 2011; Little et al. 2010).

Similarly, the *cultural-ecological moderation hypothesis* states that the attractiveness bias is most evident in individualistic settings that promote an experience of independence from context and weaker or nonexistent in settings that promote an experience of embedded interdependence (Anderson et al. 2008; Fiske 1991). Individualistic settings promote a free-market construction of social connection in which choice, attractiveness, and other determinants of preferential selection become important for social outcomes (such as friendship, mating, and employment). In less individualistic settings, attractiveness exerts less influence on interpersonal outcomes because there are fewer affordances for choice of social connections based on personal preferences. Support for this hypothesis comes from a program of research that examined both (1) the association of participant attractiveness with self-reported life outcomes and (2) effects of target attractiveness on participants' judgments of expected target outcomes across two sources of cultural-ecological variation: a comparison between participants in U.S. and

Ghanaian settings (characterized by affordances for individualism and embedded interdependence, respectively) (Anderson et al. 2008) and a comparison between participants from urban and rural settings within the United States (Plaut et al. 2009). Consistent with the hypothesis, the impact of attractiveness on outcome ratings was greater in the United States and urban settings than in Ghanaian and rural settings.

These examples of past research highlight the effects of context on the attractiveness bias. Our current research considers the impact of another contextual factor, the Internet, which is becoming increasingly prevalent in people's lives (Baym 2015; Dutta et al. 2015). Given the relatively high ease and freedom of choosing, establishing, and ending Internet-based connections, the cultural-ecological moderation hypothesis would suggest that attractiveness, as a determinant of selection, will have a larger influence on social outcomes in online than in offline contexts. Alternatively, it is possible the relatively lower salience and lower distinctiveness of physical attractiveness in online connections may decrease the attractiveness bias compared with an offline setting. Our research tests these competing predictions.

To summarize, a consideration of contextual factors for the attractiveness bias helps to illuminate the ecological foundations of mind. Preferences for attractive others interact with ecological systems that differentially afford the development of these predispositions into observed psychological habits. A complete account of the attractiveness bias must consider not only processes of natural evolution that produce genetic predispositions, but also contexts and processes of cultural evolution whereby people may (re)produce the ecological structures that afford and amplify those genetic predispositions.

Evolutionary explanations for financial and prosocial biases: Beyond mating motivation

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Abstract: Mating motivation likely plays a role in bias to attractive individuals, but there are other complementary theories drawn from the evolutionary literature related to competition, friendship, and leadership selection that also make relevant predictions concerning biases towards attractive individuals. The relative balance of these factors will be context dependent and so help explain why the pattern of bias is sometimes variable.

Attractive individuals have an advantage in social exchange, and the target article highlights the financial rewards associated with being attractive. The first part of Maestriepieri et al. focuses on sexual opportunity as a primary reason for explaining financial and prosocial biases in favour of attractive people, and this idea is supported by data. However, the same pro-attractive biases can be found when mating motivation is an unlikely explanation for their existence, such as among individuals of the same sex (Lucas & Koff 2013; Rosenblat 2008). Table 1 in the target article suggests that biases in opposite-sex pairs are greater than those in same-sex pairs, but not completely absent for the latter, and this leaves the question of why there are biases in same-sex pairs at all.

Mating motivation may result in favouring attractive individuals and, indeed, may be the strongest determinant of positive bias in opposite-sex pairs, but there are also other relevant theories that are complementary in predicting biases for and against attractive individuals in situations where mating motivation is not relevant. I argue here that evolutionary-based theories related to competition,

friendship formation, and leadership choice can help explain why biases exist between individuals of the same sex.

Maestriperieri et al. note that individuals may be concerned over the attractiveness of potential sexual rivals and so not biased in their favour, or even biased against them (Agthe et al. 2010; 2011). This direct form of competition among members of the same sex for mates is widely studied in nonhuman animals, in which it is termed *intrasexual selection* (Andersson 1994), and the same logic applies to other types of competition, such as for resources. For example, in the case of the hiring panel, the person being hired could be seen as a potential rival for promotion, not just in mating.

In opposition to the predictions for competition, pressures related to friendship formation suggest that we might favour attractiveness in same-sex alliances and friendships. Indeed, studies show that people want to bond as friends with attractive individuals (Lemay et al. 2010). Friendship bonds are important in humans because of living in groups (Dunbar 2009), and friendships are adaptive, being linked to improved reproductive success and living longer (Seyfarth & Cheney 2012). In the example of the hiring committee, they are not only selecting potential rivals, but also potential allies. If we consider that individuals may select other individuals to join not just their organisation, but also their in-group, then we can predict that they may hire more attractive individuals as potential allies and friends. For example, tall men are found to be both attractive and dominant, and a bias towards attractive other men by heterosexual men may be predicted because tall, attractive, dominant men are likely to make powerful coalitional partners and be favoured as friends and allies (Little & Roberts 2012).

Humans also often elect to follow leaders, and there are evolutionary theories concerning when it may be beneficial to an individual to decide to follow certain other individuals (Van Vugt 2006). Attractive individuals might make popular leaders because of useful traits associated with attractiveness such as health. Indeed there is evidence that attractiveness is positively related to being selected as a leader: Attractive political candidates are evaluated more positively than unattractive individuals (Budesheim & Depaola 1994), people are more likely to say they would vote for an attractive leader than a less attractive leader (Little et al. 2012), and some studies have demonstrated that attractive candidates are more likely to win real elections (Berggren et al. 2010).

For the three factors mentioned previously, attractiveness may play a role in positive financial biases towards same-sex and opposite-sex others without recourse to mating. However, these different factors are most likely complementary to mating motivation, and which factors come into play is likely to depend on the context of the particular situation. For example, the apparent conflict between predictions for attractive same-sex individuals for competition (negative) and friendship (positive) can be resolved by considering the context – is the person a threat or a potential ally? This resolution is supported by studies showing that those with high self-esteem are not biased against attractive same-sex individuals compared to those with lower self-esteem and that the desire to interact with versus avoid individuals also mediates these biases (Agthe et al. 2011). Perceived threat or competition may then underlie bias to attractive same-sex individuals, and in some contexts, such as where low threat is perceived, individuals can favour attractive same-sex individuals.

Leadership may represent a special case where issues of competition are reduced because the benefit of following particular leaders is high. In terms of context, attractive faces are relatively more valued as leaders in wartime than peacetime contexts. This pattern suggests that attractiveness, which may cue health and fitness, is perceived to be a useful attribute in wartime leaders (Little et al. 2012), but less so in peacetime leaders. In this way, leaders appear to be chosen because the characteristics they possess are seen as best suited to lead in particular situations. These “conditional” biases are important in the context of financial and prosocial biases in favour of attractive people because they highlight that the financial reward for beauty may not be

straightforward and that beauty may be rewarded more or less depending on the job or situation in question.

In summary, mating motivation likely plays a role in bias towards attractive individuals. Three complementary theories drawn from the evolutionary literature also make relevant predictions concerning biases towards attractive individuals: competition, friendship, and leadership selection. The relative balance of these different factors will be context dependent, and the effects of context can help explain why the pattern of bias towards attractive same-sex and opposite-sex others is variable. The authors have highlighted an important issue in that mating can help explain pro-attractive biases, and here I note that there is more to evolutionary explanations than sexual reproduction – evolutionary approaches also encompass ally formation, leadership, and strategic choice, which could all have an impact on financial and prosocial biases relating to appearance.

What does evolutionary theory add to stereotype theory in the explanation of attractiveness bias?

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Abstract: Maestriperieri et al. seem to put forth an argument in which they become vulnerable to some of the same criticisms that they level against stereotype theory. As a result, the explanatory utility of their account of attractiveness bias comes into question, and it is unclear whether it offers anything superior to stereotype theory in conceptual soundness.

As noted by Maestriperieri et al., social science research has documented the existence of attractiveness bias operating across a variety of domains with very little consideration being given to evolutionary explanations. Although we are in favor of evolutionary explanation in general and often see the value in separating ultimate and proximate causation (but see Laland 2015), Maestriperieri et al. seem to be putting forth an inconsistent argument in which they become vulnerable to many of the very same criticisms leveled against stereotype theory in the target article. In the light of these inconsistencies, the explanatory utility of their evolutionary account of attractiveness bias comes into question, as does the issue of whether the associated adaptationist perspective offers anything superior to the starting point of stereotype theory in conceptual soundness (Racine 2013).

Although the authors allow that additional sociocultural factors are likely to contribute to the observation of such biases, for their evolutionary perspective to make a clear contribution it should provide a degree of explanatory power above and beyond that offered by existing accounts of attractiveness bias. By contrast, Maestriperieri et al. attempt the difficult balancing act of fashioning an interdisciplinary approach while advocating for the evolutionary explanation they wish to conceptually situate front and center. It is in this act of situating their particular evolutionary explanation as a solution to, or means to overcome, some of the existing problems and criticisms in explaining attractiveness bias that the article tends to falter and theoretical issues arise surrounding the explanatory power of those evolutionary concepts invoked (Wereha & Racine 2012).

An essential component of the authors' argument in favor of considering an evolutionary explanation for attractiveness bias over extant stereotype hypotheses is that the latter lack the capacity to make claims about the causal efficacy of said stereotypes in determining preference for attractive individuals. Maestriperieri et al.

(sect. 4.1, para. 5) claim that “the motivation to behave prosocially toward attractive individuals pre-exists the attribution of positive characteristics to them and is not caused by them, as assumed by stereotype-based theories.” Using the labor market as an example, this is to say that attractive persons are not perceived by the agent as better qualified, but nonetheless are increasingly likely to receive a job offer over an unattractive counterpart. This implies that the construct (i.e., stereotype) pre-existing manifestation of attractiveness bias operates outside of the agent’s awareness insofar as subsequent attributions of positive characteristics may be seen as a post hoc rationalization. Given this implication, criticisms of causal inefficacy are ill advised because they may be leveled at the authors’ own position if it is considered problematic for a causally implicated construct to pre-exist the motivation it is hypothesized to generate (see also Slaney & Racine 2013). Similar to a stereotype, the authors write of attractiveness bias as the manifestation of a psychological adaptation, which ancestrally conferred the benefit of surrounding its possessor with an increased number of potential fertile mates. It is highly unlikely that an agent in charge of hiring new employees would acknowledge this influence of mate selection pressures on the decision process. As such, the psychological adaptation hypothesized by Maestripieri et al. must also pre-exist any attribution of positive characteristics relevant to employability and thus be ontologically situated at the same position in the causal chain as a “beautiful is good” stereotype.

When situated in the causal story in this manner, more problems with their account begin to arise. Those portions of the article drawing on outcomes of economic games that demonstrate males offer more resources to an attractive female whom they will never see again, or exhibit more generous behavior in the presence of attractive female bystanders, are intended by the authors to bolster their own evolutionary explanation while simultaneously discounting stereotype theory on the basis that a stereotype is causally inefficacious in such circumstances given the male has no possibility of future interaction with the attractive female participant/bystander. However, if the hypothetical construct of a stereotype pre-exists any attribution of positive characteristics, the potential for future interactions in which said positive characteristics may come to bear need not be considered when implicating stereotypes in instances of attractiveness bias. Conversely, if a psychological adaptation beneficial to mate selection is implicated, the possibility of future interactions with an attractive participant/bystander indeed ought to be a salient variable in manifestations of the bias.

In addition to the previously mentioned theoretical inconsistency arising from reference to economic games, the diversity of methodologies employed in those studies used to support the authors’ argument bring further problems with the ad hoc nature of their mismatch hypothesis. By combining evidence from both paradigmatic cases of attractiveness bias (e.g., preference for attractive job candidates being relatively more pronounced in males) with instances of such bias functioning to promote prosocial behavior (e.g., males’ increased generosity in the presence of attractive opposite-sex bystanders), Maestripieri et al. create potential conceptual confusion surrounding the adaptive function held responsible for said findings. In the former case, a model of male intrasexual competition for females is implied, whereas the latter relies more heavily on increasing the probability of female mate selection. For their account to be plausible, it must be specified for which mating strategy the psychological adaptation has been selected, because not all of those strategies evidenced by the social psychology findings cited were salient in the ancestral environment in which this adaptation developed.

In summary, both Maestripieri et al. and stereotype theorists hypothesize a psychological construct. As it stands, the benefit of a stereotype is its amenability to social change without ad hoc re-contextualization to capture disparate mate selection models. Although acknowledging the legitimacy of many issues identified with stereotype theory by the authors, and maintaining the usefulness of evolutionary explanation in accounting for certain instances of attractiveness bias, using it as foundational to explaining the

phenomenon seems to serve only to conceptually complicate matters. Integrating the claims of Maestripieri et al. into a dual-inheritance model not privileging psychological adaptation over sociocultural considerations may ultimately be more coherent and parsimonious (e.g., Boyd et al. 2011).

How should we tackle financial and prosocial biases against unattractive people?

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Abstract: The fact that attractive people benefit from their good looks is not bad per se. Rather, what is worrisome is the fact that unattractive people are discriminated against, and that such discrimination negatively affects many aspects of their lives. I focus on the moral implications of this discrimination and on the possible measures that could be taken to alleviate it.

As shown in the article by Maestripieri et al., being beautiful is advantageous in many realms of life, from social interactions to romantic relationships, from employment opportunities to economic success. On the other hand, it is also well documented that unattractive people are often discriminated against. “Lookism” can be defined as discrimination against people considered physically unattractive according to widespread psychobiological and/or social standards.

Although lookist practices are wide and pervasive, lookism is often dismissed by appealing to the conventional wisdom that “beauty is in the eye of the beholder.” If there is no agreement about who is beautiful and who is not, so the argument goes, then no one can systematically be discriminated against, and lookism is not “real.” There are, of course, undeniable subjective differences in aesthetic preferences, and the same feature may be considered attractive by a certain society and unattractive by a different one. However, people from different geographic areas and/or historical periods are found to mostly agree about whom they find beautiful/ugly, and they treat more favorably the attractive and discriminate against the unattractive. So, insofar as the standard for (un)attractiveness is (at least) an inter-subjective standard, if not an objective one, lookism is a real problem.

Law scholar Deborah Rhode estimates that “anywhere from 12 to 16 percent of workers believe that they have been subject to such bias, a percentage that is in the same vicinity, or greater, than those reporting gender, racial, ethnic, age, or religious prejudice” (Rhode 2010, p. 9). Economist Daniel Hamermesh suggests that African American men’s earning disadvantage is similar to the disadvantage experienced by unattractive men, and that, over a lifetime, a below average-looking man earns \$230,000 less than an attractive one (2011). Quite unsurprisingly, unattractive people have been found to be less happy than attractive ones (Hamermesh & Abrevaya 2013).

Maestripieri et al. argue that prosocial biases in favor of beauty are more likely because of sexual motives than other motives, such as for example motives related to the well-known “what is beautiful is good” bias, whereby we tend to attribute positive personality traits to attractive people (Dion et al. 1972) (in fairy tales, such a tendency is emphasized, and very often the villain is portrayed as extremely unattractive).

If Maestripieri et al. are right in their interpretation of the evolutionary origin of lookism in the workplace, and mating motives are at the core of this form of discrimination, then we have an interesting starting point for devising strategies to tackle the issue of discrimination against the unattractive.

Societal change is often supported by legal change, as testified by the case of discrimination against disabled people, black people,

women, and homosexuals. Rhode suggests that the law should extend protection to people discriminated against for their appearance; for example, the scope of anti-discriminatory legislation already in use could be broadened so as to protect the unattractive. A few cities and districts have already attempted to give protection to victims of lookism: Michigan, District of Columbia, Howard County, San Francisco, Santa Cruz, Madison, and Urbana (Rhode 2009).

Legal measures may have a broad positive effect in terms of giving visibility to a discriminatory practice and enabling unattractive people to have equal opportunities. The simple fact of officially acknowledging that lookism is a problem puts us in a better position to develop strategies to overcome it.

One field where acknowledging the problem can have beneficial effects is the job market. Job committees should start taking into account such pervasive biasing elements. For example, they could develop strategies to avoid that mating preferences of a committee member penalize the least attractive candidate of the opposite sex and/or the most attractive candidate of the same sex (according to the target article, heterosexual individuals tend to have negative biases toward attractive people of their same sex because they are potential rivals). Job interviews could be conducted via phone and not in person, or each committee member's evaluation of each candidate could be adjusted for the biases related to gender and to level of attractiveness. As far as job promotions are concerned (external, when possible) review of anonymized reports of the employees' achievements could help in assessing their merits in a more objective way.

At the level of the public health system, one strategy that could be deployed to help a person who has been formally recognized as a victim of lookism is to provide her with benefits for cosmetic interventions (from makeup classes to cosmetic surgery).

The economist Hamermesh notes that insurance companies compensate people for prospective economic loss when their facial features are negatively affected by events such as accidents and assaults; on a similar basis, we could also consider compensating people for unattractiveness-related economic loss (Hamermesh 2011).

Some of the solutions I have briefly sketched would require the unattractive person to obtain an "unattractiveness certificate." In this way, they would have objective grounds on which to claim a right to be protected by anti-discriminatory measures. Admittedly, precise evaluation of degrees of unattractiveness would be an extremely difficult task. Moreover, it is likely that people would not feel comfortable undergoing an assessment of their appearance. However, some people have already sued their employers for discriminatory practices based on looks (Corbett 2007), and even if the majority of people would not use legal measures, the fact that the law prohibits lookist practices could still be a useful deterrent.

At the same time, however, society as a whole should develop broader and more inclusive paradigms of beauty. Although evolution shaped some of our aesthetic preferences, it is also true that economic, social, and historical factors have contributed to determining the current extremely narrow paradigm of beauty.

It is important to conduct further research to understand the mechanisms at the origin of lookism. Although lookism is often considered a politically incorrect topic to discuss, it is only by learning more about it that we will be able to find ways to deal with such a phenomenon and, we hope, alleviate its negative impact.

Just My Imagination: Beauty premium and the evolved mental model

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Abstract: Imagination, an important feature of the human mind, may be at the root of the beauty premium. The evolved human capacity for simulating the real world, developed as an adaptation to a complex social environment, may offer the key to understanding this and many other aspects of human behavior.

Japan has a large-scale idol industry in which teenage girls with no significant talent are supported by their fans solely on the basis of their cute appearance. Some men purchase multiple copies of the same CD solely for the opportunity to shake hands and briefly chat with their idols at promotional events. This "Idol Otaku" represents the emergence of an extreme version of the phenomenon referred to in the target article and may be based on similar psychological mechanisms.

I agree with the argument that the beauty premium is based on attitudes related to seeking potential mates. The authors contrast a model in evolutionary psychology with ones rooted in behavioral economics and social psychology. However, the "models" proposed by behavioral economics or social psychology are simply proximate factors that were identified by Tinbergen (1963) in his famous introduction to ethology. In contrast, evolutionary psychology is concerned with ultimate factors underlying human behavior and generates models of causal mechanisms through the use of reverse engineering (Pinker 1997). That is, the differences among these academic fields amount to differences with respect to the time scales of the critical questions. Ideally, the authors should review the issue at hand within the framework of Tinbergen's four questions rather than by contrasting models across these academic disciplines.

Although an explanation of the beauty premium through sexual selection is plausible, additional factors should be considered. Indeed, as the authors have described in their discussion of error management theory, favoring beauty is most advantageous when the cost of doing so is sufficiently low. The phenomenon of Idol Otaku in Japan, however, suggests that the beauty premium is not supported by such a simple mechanism. People are sometimes willing to pay a considerable cost for attractiveness without receiving any tangible reward for doing so, as in the case of the Otaku, who spend large sums of money on young girls with whom they could never have a close relationship. I believe that imagination, which is an important characteristic of the human species, is related to this phenomenon. The beauty premium may have emerged because of an optimistic delusion that allows a person to believe that he may be able to have a close relationship with a particular attractive person even if this is impossible in the real world. This kind of imaginative activity may have developed as an adaptation in human evolutionary history.

Geary (2005) insists that human intelligence is characterized by the construction of a mental model of the outer world, a capacity that may have evolved as an adaptation to a complex social environment. Human general intelligence has evolved as a means of controlling resources required for survival and reproduction. Humans acquired the ability to control ecological variables such as food and predators through the use of tools and various other methods. As a result, the social environment in which people competed or cooperated with each other for resources, obtained through the exertion of such control, gave rise to important selective pressures. In this environment, those whose behavior was difficult to predict held an advantage over others; hence, simulations of the real world in a virtual world within one's own brain became important. Geary (2005) refers to such internal models as "autonoetic mental models." People generate mental models representing the outer world and the involvement of a present, past, or future self. According to Geary (2005, p. 235), "These are perfect worlds in which the individual is able to control other people, events, and access to material resources and to do so in ways that would have enhanced survival or reproductive outcomes during human evolution." This idea corresponds to the "Popperian creature" proposed by Dennett (1995) as a model of the evolved mind. Popperian creatures can preselect behaviors from among a variety of possible options, eliminating the truly stupid

ones in their inner virtual world before taking the risk of applying them in the harsh external environment. Compared with the “Skinnerian creature,” which can learn only by testing actions in the external environment, such that successful actions are reinforced and therefore tend to be repeated, the Popperian creature is more sophisticated and efficient (Dennett 1995). This ability to simulate the external world in an inner model may be one reason why the human species has evolved such a large and complex brain despite its significant costs (Aiello & Wheeler 1995). Excessive simulation, however, may occasionally lead to delusion. One such example is religion. Humans exhibit cognitive characteristics such as those described by theory of mind (Premack & Woodruff 1978) and pattermicity (Shermer 2011), which have allowed us to adapt to various ecological and social environments throughout human evolutionary history. These traits lead us to imagine entities that do not really exist and to attribute agency to them (Bering 2010). Such a simulation underlies the belief in a god or multiple gods. In some cases, religions require their followers to pay extreme costs, ranging from donations to suicide bombing. Religion does, however, serve the function of strengthening the cohesiveness of a group and facilitating the process of group selection, which may explain the existence of religion despite its unscientific nature and irrationality. Delusion has positive as well as negative consequences.

The ability to create a mental world that simulates actions in the external environment has an impact on many social and cultural phenomena. For example, altruism toward non-kin from whom they do not expect future help is an important behavior that is characteristic of human beings; such altruism is based on indirect reciprocity (Nowak & Sigmund 1998). Altruistic behavior toward strangers can then be interpreted as a kind of investment because a reward for the behavior is not guaranteed. Our societies, however, are sustained by this highly developed indirect reciprocity. Optimistic misinterpretations and imagination regarding the behavior of other people are needed to make such investments possible (e.g., Oda et al. 2011). The target article should, therefore, address future challenges and shed light on human behavior by appealing to the power of imagination.

The biasing effects of appearances go beyond physical attractiveness and mating motives

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Abstract: The influence of appearances goes well beyond physical attractiveness and includes the surprisingly powerful impact of “face-ism” – the tendency to stereotype individuals based on their facial features. A growing body of research has revealed that these face-based social attributions bias the outcomes of labor markets and experimental economic games in ways that are hard to explain via evolutionary mating motives.

In their review of the literature, and the arguments that follow, Maestriepieri et al. largely overlook the fact that the biasing effects of appearances go well beyond physical attractiveness and include the surprisingly powerful impact of face-based social attributions (e.g., the extent to which a person has a competent-looking or trustworthy-looking face). Missing from their article is a discussion of the role of “face-ism” – the tendency to stereotype individuals based on their facial appearances. A growing body of research has revealed that people spontaneously

form social attributions from facial cues (Todorov et al. 2015); that these face-based attributions can bias a variety of important decisions (Olivola et al. 2014b), including those made in labor market contexts and experimental economic games; and that they do so above and beyond physical attractiveness. Many of these face-ism biases are hard to reconcile with evolutionary theories and harder still to explain in terms of mating goals.

1. Face-based social attributions predict labor market outcome. There is copious evidence that individuals seem to benefit from having faces that we stereotypically associate with desirable traits (Olivola et al. 2014b; Todorov et al. 2015). Military cadets who have more dominant-looking faces achieve higher ranks (Mueller & Mazur 1996), which may help explain why military leaders have distinctively dominant (or “cold”-looking) faces relative to other types of leaders (Olivola et al. 2014a). CEOs who have more competent-looking faces receive higher compensation, despite not performing any better (Graham et al., in press); in fact, their facial competence predicts their compensation better than their facial attractiveness (Graham et al., in press). Political candidates who have more competent-looking faces receive larger vote shares during elections, after controlling for their facial attractiveness (Olivola & Todorov 2010); here too, facial competence is a better predictor of success than facial attractiveness (Olivola & Todorov 2010). Political candidates who have more conservative-looking faces are also more popular with conservative voters, despite these political facial stereotypes being unrelated to physical attractiveness (Olivola et al. 2012). People are more likely to lend or donate money to individuals who (visually) look trustworthy, after controlling for their physical attractiveness and a host of financial and demographic variables (Duarte et al. 2012; Jenq et al. 2015). Recent studies have also shown that facial trustworthiness predicts corporate status (Linke et al. 2016), and even academic research productivity (Dilger et al. 2015), to a greater extent than facial attractiveness.

2. Face-based social attributions bias decisions in experimental economic games. Research has also shown that face-ism biases choices in experimental economic games. For example, a number of studies have demonstrated that senders in the trust game invest significantly more in receivers who have trustworthy-looking faces than in those with untrustworthy-looking faces (Bailey et al. 2016; Chang et al. 2010; Ewing et al. 2015a; 2015b; Rezsescu et al. 2012; Tingley 2014; van’t Wout & Sanfey 2008). In another type of experiment, involving a “debt game” in which players had to guess whether potential lenders were going to charge them no-, moderate-, or high-interest rates on their debt, participants were more willing to borrow from lenders with trustworthy-looking faces than from those with untrustworthy-looking faces, even though these facial cues were uncorrelated with the lenders’ actual decisions (Suzuki & Suga 2010). The biasing influence of facial trustworthiness in experimental economic games is a robust phenomenon: It has been demonstrated across age groups, including young children (Ewing et al. 2015a; 2015b), young adults (Bailey et al. 2016; Chang et al. 2010; Suzuki & Suga 2010; Tingley 2014; van’t Wout & Sanfey 2008), and older adults (Bailey et al. 2016), and also across countries, including the United States (Chang et al. 2010; Tingley 2014; van’t Wout & Sanfey 2008), the United Kingdom (Rezsescu et al. 2012), Australia (Bailey et al. 2016; Ewing et al. 2015a; 2015b), and Japan (Suzuki & Suga 2010). Only children with autism spectrum disorder were shown to be immune to this bias (Ewing et al. 2015a). Moreover, this bias persists (albeit to a smaller degree) in the face of contradictory reputational information concerning the receiver’s trustworthiness (Rezsescu et al. 2012). Importantly, facial trustworthiness influences investments in the trust game even when facial attractiveness fails to do so (van’t Wout & Sanfey 2008), or when the facial stimuli have been designed to vary primarily in terms of their perceived trustworthiness (Bailey et al. 2016; Rezsescu et al. 2012; Tingley 2014).

3. The biasing effects of face-based social attributions are difficult to explain in terms of evolutionary mating motives. Although the biasing effects of physical attractiveness may be well explained in

terms of evolutionary mating motives, the same is not true of face-based trait inferences. Consider labor market outcomes: Evolutionary mating motives cannot explain why, even after controlling for physical attractiveness, face-based social attributions predict income (Graham et al., in press), professional status (Linke et al. 2016; Mueller & Mazur 1996), political success (Olivola & Todorov 2010; Olivola et al. 2012), and the ability to attract loans (Duarte et al. 2012) or donations (Jenq et al. 2015). Nor can they explain why political facial stereotypes (how conservative a political candidate's face makes him or her look) predict the voting preferences of Republicans but not Democrats (Olivola et al. 2012), despite both groups having (presumably similar) mating motives. Or consider results from the trust game: Evolutionary mating motives fail to explain why 5-year-olds and 10-year-olds (who presumably lack sexual interest) are more willing to invest in individuals who have trustworthy-looking faces (Ewing et al. 2015a; 2015b), or why adult players are more willing to invest in individuals represented by trustworthy-looking computerized faces (Bailey et al. 2016; Rezlescu et al. 2012; Tingley 2014), despite the (very) limited sexual appeal of these avatar-like face stimuli. In fact, face-based social attributions have been shown to predict mating preferences, *above and beyond* physical attractiveness (Olivola et al. 2016). In sum, researchers need to recognize that the biasing effects of appearances go well beyond physical attractiveness and mating motives.

An assessment of the mating motive explanation of the beauty premium in market-based settings

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Abstract: Labor market and real-life studies were not designed to discriminate between evolutionary and taste-based and stereotype explanations for the beauty premium, have too many confounding effects, and lack crucial information. Smaller-stake and experimental studies provide more compelling evidence in favor of mating motives and suggest the direction of future research for the economists' field studies.

Maestriperieri et al. provide an excellent compendium and careful interpretation of the various explanations proposed by economists, social psychologists, and evolutionary psychologists for the beauty premium we observe in many aspects of everyday life. In particular, the authors illustrate the advantages of the evolutionary psychology theory that attractive individuals are favored for mating reasons in explaining the evidence from labor markets to loans, political elections, and economic games in the lab.

Economists, and possibly other scholars, have so far mostly ignored such an explanation and have not directly tested it in the field. The authors have the merit, among others, of stressing the importance of such an explanation, creating an opportunity for dialogue across disciplines, and spearheading more work in markets and other high-stake settings to disentangle the evolutionary explanation from the other two being proposed.

The task that Maestriperieri et al. have embarked on is a difficult one. Despite growing evidence from field studies that attractive people get better treatment (Hamermesh 2011), are more likely to find jobs and be promoted (Hamermesh and Biddle 1994), and get better terms on loans (Ravina, under review), most of the market-based studies are designed to disentangle the taste-based discrimination explanation from the statistical discrimination/social

psychology explanation that good looks are markers of productivity and good character. As such, these studies do not usually contain sufficient analyses to directly test the evolutionary explanation. For example, findings that attractiveness matters more for women than men in employment audit studies (Busetta et al. 2013) can in principle be reconciled with the statistical discrimination explanations of higher productivity if the jobs for which this is true are more likely to be filled by women and also happen to be jobs that require a lot of interaction with the public. Although in theory the study could have been designed to estimate the importance of mating motives in employers' decisions, not enough information was collected for this purpose. For example, the study does not provide enough information to assess the actual performance of employees with those characteristics that interacted with the employers in the past. The study also does not contain information on the sex of the employers who are more biased toward attractive candidates. Finally, getting a callback is not equivalent to landing the job, and although some employers might be motivated by mating motives when deciding whom to call back, they might act differently when making job offers having more long-lasting economic consequences for their firm.

This opens the question of the strength of the mating motive as the stakes increase. The evidence in favor of the evolutionary explanation is stronger in studies where smaller amounts of money are at stake, like for charity donations, restaurant tips, mock jury trials, and essay evaluations. In such cases, it is easier to disentangle the different explanations because more information is provided about the gender of the decision maker and the attractiveness and gender of the person being evaluated, and in many cases, the individual's actual ability is accurately measured or randomly assigned (Benson et al. 1976). However, such studies involve very low stakes and artificial settings, which might abstract from factors that in real life routinely interact with the feature being studied and change its effects.

Does the mating motive survive in settings with higher stakes, different contexts, and a more heterogeneous population? From the evidence available so far, we do not have enough information to tell. In addition, several economic studies indicate that the higher the experience and expertise of the decision maker, the less influenced he or she is by appearance (see Ravina, under review, for an example). Whether the behavior toward attractive people is conscious or unconscious, when the stakes become bigger, the decision makers might pay more attention to other dimensions of the problem, focus more, and think their decisions over more carefully.

Finally, another important avenue of research that few studies touch upon is whether other factors and personal characteristics interact with gender to affect mating motivations. The findings in Jensen (2013) that dominant males are less affected by attractiveness than weak ones constitute an example in this direction. Such analysis is important because it contributes to shedding light on the magnitude of the beauty premium in different contexts and different subjects and could possibly help distinguish among the explanations put forward in the different disciplines.

Understanding the mechanism behind the beauty premium has important implications. Depending on the causes of the positive bias toward attractive people, and the relationship between attractiveness and productivity, prosocial behaviors, and personality traits, we should either ignore the bias or make sure that our employees/decision makers are made aware or protected from it and from the "mistakes" to which it leads. Understanding the mechanism will also help us identify the people more prone to the bias, the contexts in which it is stronger, and possibly the best devices to protect the decision makers from it when the stakes are high, if they do not do so already by themselves. Finally, we might want to identify the cases in which we should encourage the bias as it leads to prosocial behaviors, higher productivity, or more happiness.

To conclude, the questions of whether the results found in lab experiments and smaller-stake settings "scale up" to real-life

settings with higher stakes, different contexts, and a more heterogeneous population still stand, despite the very good job the authors did in finding studies of the effects of attractiveness in the market and in real-life settings. The analysis in the article provides a starting point and an invitation for further research on the mating explanation for the attractiveness bias, especially in market-based and real-life settings.

Attentional and affective biases for attractive females emerge early in development

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Abstract: Predominant experience with females early in development results in infants developing an attractive, female-like facial representation that guides children's attention toward and affective preferences for attractive females. When combined with increased interest in the other sex at puberty, these early emerging biases might help explain the robust prosocial and financial biases men exhibit toward attractive women during adulthood.

Maestriperi et al. present a thoughtful critique of the relevant adult literature to support their theory as to why attractive individuals, particularly attractive women, elicit favorable biases even when exposure is brief or not in person. The authors' developmental section of the paper, however, assumes infants and children show biases for attractive individuals regardless of target sex, but research indicates early emerging attentional and affective biases toward attractive females are stronger and more consistent than those toward attractive males. We propose that these biases develop as a function of children's typical social world and likely contribute to the strength of adults' prosocial and financial biases toward attractive women.

During the first year, approximately 70% of infants' experiences are with women (Rennels & Davis 2008; Sugden et al. 2014). Subsequently, infants develop perceptual expertise in processing female faces (Quinn et al. 2002; Ramsey et al. 2005) and can mentally represent female face averages (de Haan et al. 2001; Rubenstein et al. 1999), but not male face averages (Ramsey et al. 2005). Both infants and adults perceive faces similar to an average facial representation as attractive (Langlois & Roggman 1990; Rubenstein et al. 1999), but infants' female-like facial representation produces discrepancies in how attractiveness guides their attentional biases for and categorization of the two sexes. For example, by 2 to 3 months, infants look more at high relative to low attractive female faces (Langlois et al. 1987), whereas data regarding infants' interest in high attractive male faces are inconsistent (Ramsey et al. 2005). By 6 months, infants categorize female, but not male, faces based on attractiveness (Ramsey et al. 2004; Rennels et al. 2016). Hence, females' attractiveness is salient very early in development.

Predominant experience with women typically continues during the first 3 years (Kayl 2012) and, thus, during a period of significant brain growth (Knickmeyer et al. 2008), which should maintain and strengthen children's attractive female-like facial representation. Indeed, the early categories infants displayed were evident among older children; 4- and 5-year-olds more quickly and accurately categorized the sex of female faces that were high attractive, but attractiveness did not facilitate their categorization of male faces (Hoss et al. 2005). Early categorization of females, but not males, based on attractiveness is important because perceptual grouping of individuals is a necessary first step before biases can develop (Bigler & Liben 2006). Moreover,

because fluent processing elicits positive affect (Winkielman & Cacioppo 2001), infants' and children's ease in processing faces similar to an averaged, female-like representation (Quinn et al. 2002; Ramsey et al. 2005; Ramsey-Rennels & Langlois 2006) provides a means by which positive affect could become automatically associated with high attractive females, but not necessarily high attractive males.

When 3- to 11-year-olds assigned positive and negative attributes to unfamiliar peers based on their gender, race, or attractiveness, they showed bias in each domain, but their biases based on girls' attractiveness showed the largest effect size—they assigned significantly more positive attributes to attractive girls and more negative attributes to unattractive girls (Rennels & Langlois 2014). These same children were also particularly likely to believe that attractive girl targets would think positively of them (Rennels & Langlois 2015). Children's belief that attractive girls will reciprocate positive attributes should contribute to strengthening their affective preferences for attractive females. Such biases also affected how 3- to 7-year-olds processed information; they made significantly more errors identifying female characters whose attractiveness and actions were inconsistent with the "beauty is good" stereotype (e.g., a low attractive female displaying a positive behavior) versus consistent with the stereotype, but did not do the same with male characters (Ramsey & Langlois 2002). Female targets' attractiveness, therefore, affects individuals' affective and cognitive processing well before puberty.

Males' attractiveness seems to become more salient during middle childhood. Compared with 3- to 6-year-olds, 7- to 11-year-olds assigned more positive attributes to high attractive boys and more negative attributes to low attractive boys (Rennels & Langlois 2014). Between 5 and 8 years of age, children's facial representations become more differentiated, which means that instead of having a single representation for faces, they develop representations for different face categories (Short et al. 2011). Because of increased exposure to male peers at school, children may begin developing separate representations for female and male faces, which should impact their ease in processing attractive male faces and affective biases (Rennels & Langlois 2014).

During adolescence, facial representations presumably become even more differentiated, and pubertal changes result in heterosexuals' increased interest toward the other sex (Ivanova et al. 2012) and enhanced attention toward physical appearance: both female and male 14- to 16-year-olds consider attractive individuals as ideal mates for casual sexual relationships (Regan & Joshi 2003). Puberty might also contribute to intrasex competition and negative evaluations of attractive same-sex targets compared with positive evaluations of attractive other-sex targets (Agthe et al. 2013), but support for this conclusion is weak. The adolescents in this study did not show significant differences in their evaluations of high versus low attractive same-sex targets, providing little support for mating competition. Also, although adolescent boys more positively evaluated high versus low attractive young adult females, this difference was not significant when adolescent girls evaluated young adult males (Agthe et al. 2013). Early emerging attentional and affective biases for attractive females combined with heterosexual adolescents' increased interest in the other sex align well for males, but not necessarily females, which could account for these disparate results.

Attractiveness biases emerge early for female targets, but gradually for male targets. When mating interests emerge, biases toward attractive females appear more robust than those toward attractive males, particularly when males are the perceivers. Although mating interests likely contribute to displays of bias, experience-dependent biases that form during the early years when there is significant brain growth are important to consider too. The combination of the two likely contributes to why financial and prosocial biases favor attractive females more so than attractive males.

Prosocial behavior as sexual signaling

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Abstract: Maestriepieri et al. provide an important service in highlighting prosocial biases toward attractive people from a cross-disciplinary perspective. Here I comment on the conceptual and critical side of their review of evolutionary psychology studies. I propose that further work should be focused on understanding the role of signaling in prosocial behavior.

Maestriepieri et al. review cross-disciplinary approaches to understanding why we bias prosocial behavior toward attractive people. Their review should bring evolutionary psychology (EP) studies to the attention of social scientists while enlightening EP studies with a fuller appreciation of what has been done in the social sciences. However, in advancing the cause of adaptation as an explanation for prosocial biases, the treatment of EP here lacks a conceptual framework and critique. I therefore provide comments on the evolutionary approach presented.

Regarding their conceptual framework, Maestriepieri et al. consider “mating motives” as central to the evolutionary approach. Aside from this being an unfortunate term in invoking proximate mechanisms rather than adaptation, this is not a term used in EP. When discussing prosocial biases in favor of attractive people, evolutionary psychologists invoke sexual selection, the process of evolutionary change resulting from mating competition (Darwin 1871). It is notable that sexual selection is not referred to at all in the review, so the theoretical basis of the article must be considered weak.

Related to this, Maestriepieri et al. present what they say are three different evolutionary explanations. The first they call the “functional evolutionary hypothesis” (despite all evolutionary hypotheses being about function). This theory apparently holds that prosocial behavior toward attractive people “maintains proximity.” It assumes that prosocial behavior toward attractive people is deeply engrained in the human mind. Yet this simply begs the question of why prosocial behavior is engrained in the human mind. The second, referred to as a “non-functional hypothesis,” turns out to be a misunderstanding of how adaptation works on characteristics that are on average beneficial. Both are therefore in fact corollaries of their third hypothesis, which they refer to as the “sexual signaling hypothesis.”

Here we are getting closer to evolutionary psychology where it is established that helpfulness, generosity, kindness, and altruism serve as courtship displays. Nevertheless, Maestriepieri et al. fail to say anything about why helpfulness may be used as a courtship display as opposed to other behaviors. To do so, one has to invoke signaling theory: What is being signaled by prosocial behavior (Maynard Smith & Harper 2003; Roberts 1998)? Is it a costly signal demonstrating honestly that one has a high level of resources (Gintis et al. 2001)? Is it a reliable signal of future prosocial behavior? What makes someone attractive? Do signal receivers (attractive individuals) benefit directly through increased resources from the partner or indirectly from the “good genes” of a partner? These are all key to understanding the notion that individuals are more prosocial to attractive people. Otherwise, concluding that “attractiveness has intrinsic value (because attractive people have high mate value)” (sect. 4.1, para. 8) tells us no more than that we want to mate with attractive people.

There are too many misunderstandings to mention here. For example, Maestriepieri et al. say that a “preference for attractive individuals ... may not in itself increase an individual’s biological fitness” (sect. 2.1.3, para. 2), whereas in reality such a preference

should have on average increased fitness, hence the preference persists. Also, they misrepresent as reciprocity the case of signaling to sexual partners through prosocial behavior and then benefiting through mating. In fact, prosocial behavior benefits the signaler because it persuades the attractive individual to mate, while benefiting the attractive individual who gets a high-quality mate. Another example is the repeated conflation of function and mechanism. For example, they say there is an incentive to invest in attractive people, then “moreover” that the human mind is predisposed to respond to cues of mating – the second simply being a proximate consequence of the ultimate explanation.

Maestriepieri conclude with a call for recognition of functional explanations to complement mechanistic ones. A similar conclusion was reached by Tinbergen (1951), so it should not be necessary to repeat this. Sadly, this call does remain valid among those not yet enlightened by evolutionary thought (Darwin 1859). Basic misconceptions seem rife at the highest level among economists working on prosocial behavior: misunderstanding the role of evolutionary theory in generating hypotheses; claiming behavior is not adaptive, then using terms such as “other regarding preferences” as if these were explanatory; presenting descriptions of behavior (e.g., strong reciprocity) as if that were an alternative to functional explanation; not appreciating the role of “ultimate” explanation; and being “baffled” about phenomena that are well understood by others. Perhaps this is in part because economists are trying to exclude everything outside a game structure as confounding factors. In fact, reputation (Roberts 1998), specifically here in a mate choice context, may be among the most interesting factors.

Hence, this article is welcome if it helps to raise the profile of “sexual signaling” as a serious explanation for prosocial behavior alongside concepts such as reciprocity. Unfortunately, sexual selection is still looked down upon by some as a potential explanation for human cooperation, yet to evolutionary biologists, familiar with the power of sexual selection in producing the most extraordinary structures and behaviors in the natural world, it comes as no surprise that it should also be involved in prosocial behavior. There is a paradox that if one were to say to the average person that men will be more helpful toward more attractive women, then the person would say it was just common knowledge.

Nevertheless, the article should be doing more to show a way forward. For example, studies should test when we should find a bigger effect of attractiveness on men’s behavior than on women’s and when it should be similar, based on the relative strength of sexual selection in men and women (Stewart-Williams & Thomas 2013). Studies should also examine theoretically and empirically what is being signaled by prosocial behavior and what benefits signalers and receivers get. Section 3.2.2 lists and tabulates some EP studies, but we need a critical review of these in terms of procedural details (Farrelly et al. 2007). Studies should also consider the role of competition for potential partners and when we predict the greatest prosocial behavior toward attractive people will occur (Raihani & Smith 2015; Roberts 2015).

The wolf will live with the lamb

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Abstract: Maestriepieri et al. pit evolutionary psychology against social psychological and economic perspectives in a winner-take-all empirical battle. In doing so, they risk positioning evolutionary psychology as an

antagonistic interdisciplinary enterprise. We worry that such a framing may exacerbate tensions between “competing” scientific perspectives and limit evolutionary psychology’s potential to serve as a unifying core theory.

Maestriepieri et al. present a compelling case for why attractiveness wins social favor. We enjoyed the breadth of the review and found the central argument compelling. However, we were less enthused by the manner in which the authors presented other perspectives (indeed, entire disciplines) as foes to be vanquished, rather than allies in a common enterprise. Such a framing risks exacerbating perceptions of “evolutionary psychology” as an unwelcome wolf at the door.

We see little value—and potentially high costs—in pitting “social psychologists” against “evolutionary psychologists.” Social psychology describes a collection of research lines dedicated to studying topics diverse in scope, including emotion, cooperation, competition, morality, and political ideology. Evolutionary psychology describes an approach to understanding psychology, guided by a core set of theoretical principles (Buss 1995). Social psychology is a content area without a unifying theory (Kelley 2000), and evolutionary psychology is a theoretical perspective without a clearly defined content area (at least in terms of traditional psychological subdisciplines). The two are not natural (nor possible) foes in a debate regarding the underpinnings of the phenomenon the authors wish to explain.

Indeed, any account of the human capacity to perceive attractiveness relies on some evolutionary assumptions. Those assumptions might imply functionally specialized mechanisms that identify traits that, over evolutionary history, have been associated with fertility and genetic quality. Or they might imply a content-free “blank slate” that soaks up culture and stereotypes like a thirsty sponge—what Tooby and Cosmides (1992) refer to as the “Standard Social Science Model.” Neither of these perspectives is intrinsically “social psychological,” both perspectives are “evolutionary,” and both perspectives imply different testable predictions, many of which the target article authors aptly describe.

Diversity within evolutionary perspectives. Some of the resistance to evolutionary perspectives might stem from erroneous assumptions that evolutionary perspectives imply a single hypothesis—perhaps a hypothesis that seeks to explain a given psychological trait as directly promoting mating success. Consider a type of question that we, as researchers who identify as both social psychologists and evolutionary psychologists, often receive from our colleagues: What is *the* evolutionary explanation for (insert phenomenon here)? Such questions are misconceived because there is no single evolutionary explanation for social psychological phenomena. Instead, evolutionary psychology offers a type of meta-theory with the potential to subsume and organize midlevel theories and, in doing so, generate multiple competing hypotheses (for a recent example, see an exchange between Tybur et al. 2015a; 2015b; and Shook et al. 2015). We fear that using the definitive article before “evolutionary hypothesis” or “evolutionary explanation,” as the target article authors do, might exacerbate this misconception.

Consider how evolutionary psychologists could generate a number of accounts (not discussed in the target article) for the social effects of attractiveness. Such biases could stem from psychological mechanisms that function to detect and avoid infectious individuals, if attractive features provide information about an individual’s current or future infectiousness (Kurzban & Leary 2001). Or they could stem from psychological mechanisms that function to identify and target social allies who receive benefits from others, as attractive individuals do (Sell et al. 2009). Both of these perspectives are “evolutionary” alternatives to the reproductive value account presented in the target article. To be sure, the authors do not state that there is a single evolutionary explanation for the phenomenon they are analyzing, but they describe “mating motive” accounts as *the* evolutionary explanations for prosocial and financial biases. In doing so, they risk playing into the hands of evolutionary psychology’s critics, many of whom find

repeated appeals to mating motives to be narrow oversimplifications of the complexities of human behavior that they too are dedicated to investigating.

For this and other reasons, social psychology’s adoption of evolutionary theory has been slow, contentious, and fraught with misunderstandings (Park 2007). For example, evolutionary perspectives are often erroneously associated with an activist conservative political agenda (Tybur et al. 2007), a political agenda at odds with social psychology’s overwhelming liberalness (Inbar & Lammers 2012). Hence, evolutionary psychology can be viewed as a hostile enterprise—a wolf at the door—competing with social psychologists for grant funding, journal space, and Ph.D. students. This slows the conversation, limits knowledge exchange, and restricts the integration of empirical findings from “competing” subdisciplines.

In the current instance, evolutionary theory is not in competition with (some) economists’ taste-based discrimination model of the social advantages attractiveness affords, nor with (some) social psychologists’ stereotype-based accounts. Instead, it provides an ontologically based foundation for interpreting why these tastes and stereotypes exist in the first place. Evolutionary psychology, in general, provides a grounded distal framework, but it requires proximal mechanisms as proof of concept. If perceptions of attractiveness—and resulting behaviors—are adaptations, then they should elicit behavior that is “adaptive.” Among others, positive stereotypes and taste preferences serve this function. They complement the motivational state piqued by physical attraction, and they provide a proximal trigger for adaptive behaviors, such as increased acts of prosociality (Jensen-Campbell et al. 1995). By themselves, positive stereotypes and taste preferences cannot explain the relationship between attractiveness and prosociality at any fundamental level. They are interesting observations, but they are more interesting, more navigable, and more integrated in the light of an overarching theory of human behavior such as evolutionary psychology provides.

Despite its promise, evolutionary psychology has at times been annexed in the literature as a precocious new kid on the block. Evolutionary psychologists have sometimes responded to such rejection by investing in research that seeks to offer simple “proofs” that evolutionary theory has some role in explaining human psychology (see mating motives). For the field of psychology at large, this dynamic slows our ability to harness the power of a unified theory of human behavior. Such a theory, evolutionary or otherwise, could span the boundaries of the ever-increasing subdisciplines, increasing diversity of thought and limiting groupthink. In short, the offering by Maestriepieri et al. highlighted for us that psychological science might be better advanced were the wolf to live among the lambs.

Attractiveness bias: A cognitive explanation

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Abstract: According to cognitive averaging theory, preferences for attractive faces result from their similarity to facial prototypes, the categorical central tendencies of a population of faces. Prototypical faces are processed more fluently, resulting in increased positive affect in the viewer.

Maestriepieri et al. argue that attractive people receive higher financial remuneration because they are preferred as sexual partners. Although we agree that the available evidence shows that

attractive people make more money than unattractive people, we suggest that differences between attractive and unattractive people do not necessarily mean that there are biases *in favor of* attractive people (as opposed to *against* unattractive people) and that there are explanations for attractiveness-related bias other than those examined by Maestriepieri et al.

First, most of the research cited in the review defines attractiveness as a dichotomous variable, using only high and low levels of attractiveness. Therefore, the review cannot determine whether the effects are driven by a positive, beauty-is-good response, as the authors argue, or by a negative, ugly-is-bad response. Ugly-is-bad bias has been found in other research (e.g., Griffin & Langlois 2006; Zebrowitz & Rhodes 2004). Only research that includes a control or baseline group of medium attractive people can distinguish between these two alternatives.

Second, even young infants seem to prefer attractive faces (Langlois et al. 1987), and adult heterosexuals choose attractive same-sex partners as friends (Langlois et al. 2000). Research on ugly-is-bad bias, infant research, and research on same-sex preferences for attractive others are not consistent with most versions of mating strategy.

As to explanatory mechanism, we propose that a domain general information processing system, cognitive averaging, results in preferences for attractive faces. In the initial study of cognitive averaging theory, Langlois and Roggman (1990) mathematically averaged 32 individual female faces together to create a female face morph/blend and 32 individual male faces to create a male face morph/blend. The morphed faces increased in judged attractiveness as more faces were added. Even when created with independent sets of 32 individual faces, the morphs look quite similar to one another, suggesting that a 32-face morph is a prototype of an adult face. Both averaged and attractive faces may be perceived as prototypes and, thus, seem more familiar to the viewer, even if the face is novel (Langlois et al. 1994). Faces that represent the mathematical average or central tendency of a population (e.g., male or female) also seem more typical and to be “better examples” of a face and therefore are preferred. In addition, faces whose structure approximates the mathematical average facial configuration of a population are more fluently processed than faces distant from the central tendency. Fluent processing produces positive affect, which could explain why attractive people are perceived more positively and hold better jobs with higher salaries. Humans automatically create prototypes of faces, and even infants can abstract prototypes from individual exemplars (Rubenstein et al. 1999; Strauss 1979).

Multiple studies with adults have provided evidence that high attractive, prototypical faces are more fluently processed than low attractive, nonprototypical faces. Averaged and high attractive faces rated low in distinctiveness (a subjective measure of typicality) are categorized faster than low attractive, high distinctive faces in a species categorization task (Trujillo et al. 2014). Attractiveness facilitates the speed and accuracy of gender-based face classification (Hoss et al. 2005). Moreover, prototypicality predicts perceptual fluency and increased liking for non-face stimuli as well. Dot patterns and geometric shapes are judged to be more attractive and are more rapidly categorized when they are close to the prototype (Posner & Keele 1968; Winkielman et al. 2006). In addition, perceiving and processing prototypical faces and dot patterns requires fewer neural resources compared with perceiving nonprototypical stimuli (Leopold et al. 2006; Löffler et al. 2005; P. J. Reber et al. 1998; Trujillo et al. 2014); such a reduction in neural resource use is a hallmark of perceptual fluency.

Importantly, the fluent processing accorded by prototypicality leads to more favorable judgments of perceived stimuli (Winkielman et al. 2006) and also influences affective states. R. Reber et al. (1998) argue that fluency is in itself pleasant. Studies that have experimentally manipulated fluency (e.g., Monahan et al. 2000; Zajonc 2001) have found that increased levels of fluency augment overall mood and increase generalized positive affect.

Beyond faces and dot patterns, participants show preferences for prototypicality in many other types of stimuli, including color patches (Martindale & Moore 1988), music (Repp 1997), cubist paintings (Hekkert & Van Wieringen 1990), and voices (Bruckert et al. 2010), likely because of the ease in processing stimuli closest to the prototype. The wide variety of stimuli that conform to this prototypicality or averaging effect suggest that an evolved domain general mechanism such as cognitive averaging is a more likely explanation for attractiveness preferences than a domain-specific mechanism such as mate selection.

Tinbergen’s “four questions” provides a formal framework for a more complete understanding of prosocial biases in favour of attractive people

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Abstract: We adopt Tinbergen’s (1963) “four questions” approach to strengthen the criticism by Maestriepieri et al. of the non-evolutionary accounts of favouritism toward attractive individuals, by showing which levels of explanation are lacking in these accounts. We also use this approach to propose ways in which the evolutionary account may be extended and strengthened.

In their thorough and insightful article, Maestriepieri et al. summarise evidence comparing the dominant economic, social, and evolutionary explanations for the social and employment biases favouring attractive individuals. They justifiably conclude that these biases are better explained by an evolutionary theory (relating to access to high-quality mating partners) than they are by theories put forward by economists and social psychologists.

The authors’ argument implicitly invokes Tinbergen’s (1963) four levels of explanation (“Tinbergen’s four questions”). Tinbergen argued that complete accounts of behaviour comprise four levels of explanation: the (1) *causal* mechanism and (2) lifetime development (*ontogeny*) of the behaviour (both proximate explanations), and the (3) adaptive *function* and (4) *phylogenetic* origin of the behaviour (both ultimate level explanations). Explicitly applying a Tinbergian perspective to the authors’ arguments reveals that the authors’ evolutionary theory is the preferred option of those theories considered because it is the only one providing an ultimate, in this case, *functional*, explanation. The authors’ evolutionary theory both considered the adaptive function and made predictions about the causal mechanisms of the behaviour. The other theories are strictly proximate explanations, describing only the causal mechanism of the behaviour. This is why Maestriepieri et al. describe the social and economic theories as descriptive – proximate theories frequently are, as they describe *how* behaviours develop and manifest in an immediate sense. But when seeking to understand *why* behavioural mechanisms develop and manifest the way they do, only an ultimate-level explanation will do.

The authors' theory focuses on an ultimate (functional) explanation for favouring attractive individuals. The authors have, however, overlooked the potential utility of considering phylogenetic and comparative evidence – the other half of the ultimate-level explanation. Although non-human species do not interview applicants for jobs, choice of social partners for cooperative enterprises is an area where the authors' "mating opportunity" theory could be tested against comparative evidence. One starting point may be the acceptance or rejection of new individuals into groups in social species. For example, female chimpanzees disperse into new groups at times of high reproductive value (during oestrus and at late adolescence); they risk attack from resident females during the migration process; and resident males will defend immigrant females who are in oestrus (possibly as a way to elicit mating) (Hemelrijk et al. 1992; but see Hemelrijk et al. 1999), but attack immigrant females who are not in oestrus (Nishida 1989). Such comparisons may reveal important similarities and differences between humans and chimpanzees in prosocial treatment of high mate-quality individuals, thus providing clues to both the evolutionary precursors of the human attractiveness bias and the more recent selection pressures that may have shaped it.

A formal application of Tinbergen's framework also reveals that some of the evidence presented as support for the authors' evolutionary theory is not necessarily relevant to it. For example, the evidence reviewed of brain areas activated by attractive opposite-sex faces is no more consistent with an evolutionary explanation than it is with any of the other explanations (even if the proponents of other theories are less likely to look for such evidence). It is important to understand which brain areas are involved in perceiving facial attractiveness, and informative to know that attractive opposite-sex faces (for heterosexual observers) activate neural reward circuitry. However, all of this is evidence only of the proximate, causal mechanisms involved in making attractiveness judgements, and all of the other theories reviewed by the authors are proximate, causal theories, which could as easily incorporate this evidence as could the evolutionary theory for which they argue.

We agree with the authors that evolutionary explanations are crucial for any comprehensive explanation of the attractiveness bias. The evidence that mating motivations play an important role in these biases is strong and well articulated by the authors. Some of the evidence put forward, however, is actually difficult to reconcile with mating motivations being the sole ultimate explanation for prosocial attractiveness biases. For example, the mating motivations theory is not obviously consistent with biases favouring attractive children and same-sex individuals (because they are not potential mates). Such biases suggest that attractive individuals might also be favoured for nonmating functions, perhaps because facial attractiveness serves as a reliable cue to a range of desirable traits, and forming coalitions with, or doing favours for, such individuals confers other kinds of advantages. The authors argue against some of these possibilities, but there is a positive correlation between intelligence and attractiveness (Kanazawa 2011), for example, and if attractiveness is a cue to health (see Stephen & Tan 2015 for a review) and developmental stability (Perrett et al. 1999), as the mating motivation theory suggests, then it is likely to also correlate with other traits that are useful in social partners. If modern hiring decisions had analogues in the social dynamics of pre-industrial or pre-agricultural human societies, then favouring attractive individuals in these situations might have been advantageous. One way of testing this possibility would be to examine how widespread preferences for attractive individuals are in modern human groups across a broad spectrum of cultures and levels of industrialisation.

West-Eberhard (2014) provides a cogent summary of the complexity of behaviours expected to appear under social selection pressures (where social selection encompasses sexual selection, but includes inter-individual competition over any kind of resource, not just potential mates). In this vein, it would be

worth examining whether there are systematic patterns, beyond the opposite-sex biases towards (and, in some cases, same-sex biases against) attractive individuals. Perhaps the effects are stronger in jobs requiring extensive teamwork, or for positions where the target individual's competency is especially important, or even for positions where the target individual's attractiveness may benefit the employer directly through the attractiveness bias the target will elicit in others (for example, it may be beneficial to hire attractive salespeople, mating motivations of the hiring team aside).

Authors' Response

Moving forward with interdisciplinary research on attractiveness-related biases

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Abstract: In our response, we review and address the comments on our target article made in the 25 commentaries. First, we review and discuss the commentaries that recognized the value of our approach, accepted the main premises and conclusions of our target article, and suggested further avenues for research on attractiveness-related biases. We then respond to commentators who either misinterpreted some parts of our target article or made statements with which we disagree. These commentaries provided us with an opportunity to clarify some aspects of our target article, for example, the fact that we address both the functional significance of attractiveness-related biases and their underlying mechanisms. We provide a rebuttal to two commentaries, in which we are accused of poor scholarship. We conclude our response by addressing two commentaries that discussed the societal implications of the occurrence of attractiveness-related biases in the labor market by briefly discussing the relationship between scientific research and social policy.

The future of human behavioral research is interdisciplinary. Many aspects of human behavior are of interest to scholars in different disciplines such as psychology, biology, economics, anthropology, sociology, and psychiatry. Each of these disciplines has its own historical tradition of thought, its own methodological preferences, and its own scientific conferences and journals. We live in a globalized digital era, however, in which it is much easier than ever before to familiarize ourselves with research conducted in the past by people in the same or other countries and published in "hard to find" specialized journals. It is therefore no longer acceptable that scholars who conduct research on the same aspects of human behavior ignore the research conducted by scholars in other disciplines for historical, methodological, ideological, or practical reasons. It is also not acceptable that research conducted in other disciplines be misinterpreted or dismissed because of lack of adequate

consideration. Researchers in different behavioral disciplines must engage with each other, but also with researchers in nonbehavioral disciplines. For example, although some research conducted by evolutionary biologists, neuroscientists, geneticists, or endocrinologists does not address human behavior directly, it can nevertheless help elucidate the evolutionary history or biological regulation of human behavioral processes. Ours is not a call for some disciplines to take over others. It is simply a call for recognition that human behavior is complex and multifaceted, and therefore, it can be fully understood only by considering and integrating multiple perspectives.

The occurrence of financial and prosocial biases in favor of attractive people is a phenomenon of great interest to scholars in different behavioral disciplines. Such biases can also affect the lives of many people in modern human societies. Previous research in this area has suffered from the lack of awareness and integration of multiple perspectives offered by different disciplines and by research conducted at different levels of analysis. We are pleased that our target article has stimulated commentaries by economists, psychologists, biologists, and philosophers, among others. We hope that future research in this area will be truly interdisciplinary and will not be hampered by lack of communication or lack of respect between scholars in different disciplines, by misunderstandings about the relationship between science and society, by political correctness, or by anything else that has nothing to do with the scientific pursuit of knowledge.

R1. Expanding the research

Many commentators praised our target article, recognized the value of our approach, accepted our basic premises and conclusions, and suggested future avenues for research on attractiveness-related biases. We welcome these suggestions and hope that both our target article and these commentaries will stimulate and guide future research in this area. **Agthe & Maner** cite additional studies that support our conclusions (a) that financial and prosocial biases in favor of attractive adults are stronger for individuals who are potential mating partners, (b) that physically attractive mating partners have higher reproductive value, and (c) that the psychological, neural, and neuroendocrine mechanisms underlying favorable biases toward attractive individuals have likely been shaped by natural selection. They recommend that future research take into consideration boundary conditions for mating-related biases in favor of attractive individuals, such as the moderating influence of being in a committed relationship, one's tendency for sexual promiscuity, women's phase of the menstrual cycle, individuals' ethnic background, culture, family expectations, kinship rules, and the extent of individual choice that is allowed in personal relationships.

Lee, Adams, Li, & Gillath (Lee et al.) make many similar points, highlighting the importance of considering the influence of relationship status, sex ratio, pathogen prevalence, and individualistic versus more collectivistic cultures and settings. **Agthe & Maner** also highlight the importance of considering both mate attraction and mate competition, as physical attractiveness sometimes leads to negative, rather than positive, interpersonal judgments and outcomes (**Roberts** makes a similar point, too). They

point to research showing that negative reactions toward attractive same-sex individuals are displayed particularly by people who are likely to fear intrasexual competition.

Similar to **Agthe & Maner**, **Little** and **Buunk** recommend that future research on attractiveness-related biases should further explore both same-sex mate competition, in which attractive individuals are perceived as sexual rivals, and same-sex sexual collaboration, in which an individual strategically associates with a better-looking same-sex individual to enhance his or her potential to attract highly valued mates. **Buunk** also underscores the importance of examining physical attractiveness of potential mates in relation to other characteristics such as dominance (**Ravina** makes the same suggestion). **Le Lec, Alexopoulos, Boulu-Reshef, Fayant, Zenasni, Lubart, & Jacquemet (Le Lec et al.)** recommend that the influence of attractiveness on decision making be further explored in the context of a general model of courtship behavior, which takes into account not only the benefit of mating with an attractive individual, but also the probability of doing so in relation to one's own attractiveness, competition, and other variables. **Ravina** suggests that financial biases in favor of attractive individuals should be examined both in contexts in which the stakes are high and those in which they are low, with the hypothesis that they may be stronger in the latter than in the former case. **Ravina** also suggests that future research should investigate the experience and the expertise of decision makers, as this variable may have an important moderating influence on attractiveness-related biases, especially in the labor market.

Stephen, Burke, & Sulikowski (Stephen et al.) suggest that the attractiveness of high-quality individuals as potential mates should also be investigated from a comparative perspective, for example, by studying chimpanzees, as this analysis could elucidate both the evolutionary precursors of the human attractiveness bias and the more recent selection pressures that may have shaped it. They also advocate more cross-cultural studies of attractiveness-related biases in industrial and non-industrial societies. Finally, future studies should explore whether attractiveness-related biases in the labor market vary in relation to different professional fields or types of jobs. Building on the notion that prosocial behavior toward attractive individuals can be interpreted as sexual courtship, **Farrelly** suggests that research on attractiveness-related biases could be expanded with more detailed analyses of the role of prosocial behavior in courtship and mate choice. For example, he cites recent research showing that courtship involving prosocial behavior is particularly important in the context of long-term relationships. Both **Farrelly** and **Roberts** suggest that further research is needed to better understand the signaling function of prosocial behavior in the context of sexual courtship. According to **Hurlemann, Scheele, Maier, & Schultz (Hurlemann et al.)**, future research should also address the role of oxytocin as a possible physiological mechanism underlying the attractiveness-related biases in prosocial behavior.

We agree with **Barclay** that biological market theory can provide a powerful theoretical framework that could guide future research on prosocial and financial biases in favor of attractive adults. **Barclay** makes four important predictions that could be empirically tested: attractiveness should matter less in environments where everyone is attractive; attractiveness biases should be greater in environments

where physical attractiveness is in high demand or low supply; mating-related attractiveness biases should be greater in single men than in men who are married, raising children, sexually unreceptive, or chaste; and these biases should be especially strong in individuals who are themselves highly attractive (a prediction for which there is already some supporting evidence). Barclay also points out that just as physical attractiveness gives adults high value in the mating market, other characteristics such as high status, wealth, competence, and trustworthiness give individuals high value in other social markets in which partner choice is regulated by the laws of supply and demand.

Similar to **Barclay, Eisenbruch, Lukaszewski, & Roney (Eisenbruch et al.)** advocate a broader partner choice framework for future research on attractiveness-related biases. They argue that physical attractiveness can make individuals valuable not only in mating markets, but also in markets for business or coalition partners, friends, leaders, or followers. **Little** and **Ronay & Tybur** make the same point. Eisenbruch et al. argue that attractiveness may be associated with longevity, continued ability to extract resources from the environment, and low risk of transmitting pathogens, all of which are valuable in multiple types of social markets. We agree with Eisenbruch et al., **Little, Ronay & Tybur**, and **Stephen et al.** that evolutionary studies of attractiveness-related biases should not limit their focus on its role in mating partner choice, and that characteristics such as attractiveness, health, longevity, status, and strength, which make individuals valuable in different social markets, are often interrelated. For example, **Little** notes that tall men are found to be both attractive and dominant, and a bias toward other attractive men by heterosexual men may be predicted because tall, attractive, dominant men are likely to make powerful coalitional partners and be favored as friends and allies. We believe, however, that although the value of attractiveness in mating markets is clear, the role of attractiveness in the choice for coalition partners, leaders, or cooperative partners remains to be elucidated. In markets for coalition partners or leaders, physical strength, high status, and resources are clearly crucial, whereas in markets for cooperative partners, personality and behavior are crucial (e.g., whether an individual is trustworthy and generous). Although attractive individuals may sometimes possess these other valuable attributes, many studies reviewed in our target article indicate that attractive individuals tend to behave in a selfish and manipulative way in economic games.

Little suggests that attractive individuals might make popular leaders because of the association between attractiveness and health. However, if attractive individuals were not also physically and psychologically strong, high status, and in possession of material and social resources (e.g., political support), it is not immediately obvious that their health alone would make them appealing for a leadership position. A man may be extremely healthy and have a beautiful face; however, if he is very short, does not have well-developed musculature, is financially poor, has low status, has no social or political support, and is extremely shy, he would not be appealing as a coalition partner or a leader.

Becker highlights the need for further research on the cognitive processes underlying attentional and memory biases toward beautiful faces, emphasizing that our functional, mating-related perspective can provide a powerful

framework for guiding this research. According to **Becker**, our functional perspective can explain the finding that although physically attractive male and female faces both garner more attention, the long-term encoding of individuating features favors attractive women but not men. **Becker** suggests that cognitive biases toward the attractive faces of potential mating partners “could be largely automatic and could readily produce biases in hiring, and so forth, even when proximity/mating is not an explicit goal” (para. 6). He continues:

If attractiveness is understood as a set of visual signals of mate quality, this grounds the meaning of attractiveness in mating-related instincts and yields falsifiable explanations of both attention and memory effects, which contribute to the behavioral biases discussed in the target article. This also yields a reciprocal grounding of unattractiveness, and we should be open to the possibility that some of these behavioral effects may be more about evolved mechanisms for avoiding socially costly (e.g., unhealthy) coalition partners. (para. 6)

We agree with **Becker, Olivola & Todorov** recommend that research on the influence of facial attractiveness on decision making be linked to the large body of work investigating face-based social attributions. We briefly mentioned this research in our target article, but believe that it is only indirectly related to the main questions we addressed in our article. We agree with **Olivola & Todorov** that “Although the biasing effects of physical attractiveness may be well explained in terms of evolutionary mating motives, the same is not true of face-based trait inferences” (sect. 3, para. 1).

R2. The issue with children

The notion that attractive individuals make valuable partners also in nonmating contexts is relevant to the discussion of biases in favor of attractive children. We addressed this issue in our target article, and it was also raised by several commentators (**Stephen et al.**, **Chen, Rennels & Verba**, and **Schein, Trujillo, & Langlois [Schein et al.]**). We reiterate that biases in favor of attractive infants and children (and adolescents), as well as those shown by infants, children, and adolescents, are consistent with and do not contradict the theoretical stance taken in our target article (as argued by some commentators, e.g., **Schein et al.**). We argued that in infants and children, as in adults, physical attractiveness is probably an indicator of genetic or phenotypic quality.

Many cases of adult biases in favor of attractive children can be explained with the differential parental solicitude model, which predicts that parents should invest more in higher-quality offspring. We also hypothesized that the same neural and neuroendocrine mechanisms that regulate perceptual and behavioral biases toward attractive children from a parental motivation perspective also regulate perceptual and behavioral biases toward attractive adolescents and adults from a mating motivation perspective. The same can be said about the biases shown by prepubertal adolescents toward same-age peers or adults. It is very likely that the same neural mechanism in the human mind is responsible for positive biases toward attractive others at any age.

Consistent with our view, **Becker** argues that mating-related biases in favor of attractive adults can arise from cognitive processing biases that develop early in life.

Attractiveness-related positive biases shown at different ages are all essentially the same phenomenon – human beings are predisposed to respond to attractiveness as a marker of quality – but this phenomenon acquires different functional significance in different contexts (e.g., survival, parental investment, mating, and reproduction), with the mating function becoming preponderant in adulthood. This view is consistent with those of many of our commentators, including those who have discussed children such as **Chen, Stephen et al., Rennels & Verba**, and Becker.

Rennels & Verba cite and discuss research showing that attentional and affective biases toward attractive females are stronger and more consistent than those toward attractive males already in infancy and childhood. Similar to what we suggest in our target article, Rennels & Verba propose that these early biases contribute to the strength of adult men's prosocial and financial biases toward attractive women, which from puberty on acquire functional significance in a mating context. Similarly, **Becker** suggests that attentional vigilance to signs of genetic fitness such as facial attractiveness should emerge “even in children without mature mating motivations, because such attention facilitates the building of internal representation systems that will later form the multidimensional ‘mating space’” (para. 3). He states:

The resulting representational system can then, at the onset of puberty, facilitate both mate pursuit and acquisition, as well as promote an awareness of one's own mate status, the recognition of reciprocal mating interest, and vigilance to same-sex competitors with the greatest ability to poach our romantic partners. Adult attention is hence a symptom of long-standing habits of adaptive information pickup of mating affordances. (para. 3)

R3. Misunderstandings and disagreements

Some commentators misinterpreted what we wrote in our target article and/or made statements in their commentaries with which we do not agree. A case in point is the commentary by **Dang**. Dang writes that “there was plenty of evidence suggesting no relationship between attractiveness and biological fitness” (para. 2). We are skeptical of statements like this, which suggest that the null hypothesis can be proved. We also believe that the association between physical attractiveness (e.g., as indicated by symmetry) and biological fitness is well established in evolutionary biology, with supporting data coming from plants, nonhuman animals, and humans. Dang contends:

[T]his reasoning at the same time would greatly corrode the critiques by Maestripieri et al. of explanations provided by economists and social psychologists. This is because the most critical evidence they cited to challenge these explanations was that in reality there is little or no evidence that attractive individuals are more productive, trustworthy, and competent, although people do exhibit an attractiveness halo, just as they perceive attractive persons as having higher biological fitness. (para. 3)

Dang misunderstands the theories we discussed: The explanations provided by economists and social psychologists indeed rely on the assumptions that people *perceive* attractive individuals to be more intelligent, trustworthy, competent, and so forth. Our functional evolutionary hypothesis, however, does not imply that people *perceive* attractive individuals as having higher biological fitness. Our preference for attractive individuals as potential

mates has likely been shaped by natural selection because of the correlation between attractiveness and fitness (i.e., individuals who were genetically predisposed to be attracted to good-looking individuals and mated with them produced more and healthier offspring). Organisms are predisposed to respond to cues of fitness, not to consciously perceive the fitness value of other individuals, just as they are predisposed to behave in an adaptive way without consciously perceiving the adaptive value of their own behavior.

Dang writes that “the latent variable (i.e., mating goal) assumed by Maestripieri et al. seems like a river without headwaters or a tree without roots, given the insignificant effect even for explicit and direct manipulation of this variable” (para. 4). When we speak of “mating motives” in our target article, we emphasize that the functional significance of attractiveness-related prosocial and financial biases is related to mating. Although in some cases individuals who express positive biases in favor of attractive individuals are actually motivated to mate with them, in other cases such biases can be expressed in the absence of conscious mating motivation (**Becker** makes this point too), thus explaining why manipulating mating goals may not always necessarily influence attractiveness-related biases. For example, a happily married man may have no motivation to mate with an attractive woman and risk compromising his marriage, yet he might still behave prosocially toward this woman because his mind is predisposed to do that. Similarly, we respond to visual and gustatory cues of attractive food even in the absence of motivation to eat.

Dang states: “Maestripieri et al. relied on the evolutionary explanation to predict higher biases in favor of attractive same-sex individuals for homosexuals. This seems problematic because there is no reason to assume a relationship between homosexuality and gene passing” (para. 5). The minds of homosexual individuals are predisposed to respond to cues of fitness in potential mates just like those of heterosexuals. Men become sexually aroused and ejaculate in response to pornography even though there is no relationship between masturbation with pornography and gene passing. Dang writes that “facial attractiveness is highly dependent on sociocultural factors such as mass media influence and cultural transmission” (para. 6). These sociocultural influences exist, yet beautiful faces are universally recognized as such.

Dang argues that attraction to beautiful faces is the result of perceptual and cognitive mechanisms that have nothing to do with the signaling of genetic quality. He writes that “because of the rewarding property of attractiveness, in the labor market or economic games, attractive individuals would generally be treated better, especially when there is a potential chance for treaters who are in pursuit of a stimulating sexual experience” (para. 6). Here Dang is confusing issues of mechanisms and function. We agree that from a mechanistic perspective beautiful faces have rewarding properties, which drive individuals' preferences for these faces. This is perfectly compatible with a functional explanation of these rewarding properties and preferences in terms of mating and fitness.

Hafenbrädl & Dana argue that mating motives are not sufficient to explain the persistence of attractiveness-related biases in the labor market because, in a competitive market, firms without these biases will outcompete biased firms and eventually the beauty premium effect will be wiped out. We do not share Hafenbrädl & Dana's optimism

about the power of the market to self-correct any biases in hiring on the basis of competitive mechanisms alone. Attractiveness-related biases in decision making reflect a basic expression of human nature; they are widespread, presumably convey advantages to the individuals who express these biases, though not necessarily to their firms, and are unlikely to be wiped out by competitive market forces. Take nepotism in hiring practices as a similar case; although nepotism often results in the hiring of related but lower-quality individuals over unrelated higher-quality individuals, nepotism has been around for thousands of years in all markets around the world, and it is not disappearing anytime soon.

Hafenbrädl & Dana remark that the idea that attractiveness is correlated with desirable but unobserved qualities such as genetic quality coincides with the economic concept of statistical discrimination. They then argue that just as people can reliably assess that attractive individuals have greater genetic quality and health, they should also be able to reliably assess that they are better workers. We disagree. In one case, the attractiveness-quality link and the preference for attractive individuals as mating partners have been established by natural selection over millions of years. In the other case, human beings try to establish the competence of potential employees based on a quick look at their faces. Human beings are more likely to be wrong in their perceptions of other human beings than natural selection is more likely to have made mistakes over millions of years. The question of whether attractive individuals are better workers is an empirical one; the empirical studies we reviewed in our article suggest that they are not. We agree with **Hafenbrädl & Dana** that “they need not even be right in their beliefs that attractive workers are, on average, better for statistical discrimination to operate” (sect. 2, para. 2). This, however, begs the question of why people have the mistaken belief that attractive individuals are better workers. We believe that our target article provides the most likely answer to this question.

We agree with **Hafenbrädl & Dana** that mating motives cannot supplant all other explanations of the beauty premium, including economic ones. In fact, the evolutionary explanations we discussed in our article are broadly compatible with the economists’ taste-based discrimination model. They both assume that people have a preference for attractive individuals regardless of their personality or behavior. However, the taste-based discrimination model is so general and vague as to be useless when trying to understand the origins of preferences for attractive individuals.

Similar to **Hafenbrädl & Dana**, **Le Lec et al.** believe that we were too quick in rejecting economic and stereotype-based explanations of attractiveness-related biases. For example, they argue that as stereotypes operate most of the time on an unconscious level and their influence cannot be captured through explicit self-reports, evidence from studies that failed to demonstrate a causal role for stereotypes in attractiveness-related biases should be taken with caution. We are all in favor of caution, but stereotype-based explanations of attractiveness-related biases are accepted uncritically by many social psychologists and economists in the absence of any scientific evidence supporting these theories and without even considering alternative explanations.

We disagree with almost everything **Roberts** has written in his commentary. He writes that “Maestriepieri et al. consider ‘mating motives’ as central to the evolutionary approach. Aside from this being an unfortunate term in invoking proximate mechanisms rather than adaptation, this is not a term used in EP [evolutionary psychology]” (para. 2). In reality, a central assumption of evolutionary psychology is that adaptation occurs at the level of psychological mechanisms (e.g., perception, emotion, motivation, and cognition) rather than behavior. “Mating motives” is an expression commonly used in evolutionary psychology (e.g., see commentary by **Agthe & Maner**).

Roberts also states: “It is notable that sexual selection is not referred to at all in the review, so the theoretical basis of the article must be considered weak” (para. 2). Sexual selection is an evolutionary process, whereas our target article focuses on adaptation, the product of sexual or natural selection, and not on the process itself. **Roberts** also misunderstands the three evolutionary hypotheses we discuss in our target article. He writes:

The first they call the “functional evolutionary hypothesis” (despite all evolutionary hypotheses being about function). This theory apparently holds that prosocial behavior towards attractive people “maintains proximity.” It assumes that prosocial behavior toward attractive people is deeply engrained in the human mind. Yet this simply begs the question of why prosocial behavior is engrained in the human mind. (para. 3)

We clearly stated that according to the functional evolutionary hypothesis, attractiveness-related biases serve to maintain proximity to attractive individuals, which in turn may increase the probability of mating with them. **Roberts** continues: “The second, referred to as a ‘nonfunctional hypothesis,’ turns out to be a misunderstanding of how adaptation works on characteristics that are on average beneficial” (para. 3). No, the by-product hypothesis is not a misunderstanding of how adaptation works. By-product explanations are clearly described in evolutionary psychology textbooks. **Roberts** goes on to say that “both are therefore in fact corollaries of their third hypothesis, which they refer to as the ‘sexual signaling hypothesis” (para. 3). No, the functional evolutionary hypothesis and the by-product hypothesis are not corollaries of the sexual signaling hypothesis because they do not assume that attractiveness-related biases have a signaling function.

Roberts contends: “There are too many misunderstandings to mention here. For example, Maestriepieri et al. say that a ‘preference for attractive individuals ... may not in itself increase an individual’s biological fitness’ (sect. 2.1.3, para. 2), whereas in reality such a preference should have on average increased fitness, hence the preference persists” (para. 5). There is no misunderstanding on our part. We wrote:

A preference for attractive individuals as potential sexual partners may not in itself increase an individual’s biological fitness (e.g., if it involves same-sex individuals); however, it is likely that over the course of our evolutionary history this preference was selected for because it increased the probability of reproducing with individuals who were healthier, stronger, more fertile, or better able to invest in offspring. (sect. 2.1.3, para. 2, of the target article)

Roberts claims that we repeatedly conflate mechanisms and function. We do not. We do agree with **Roberts** on one point though: that economists often ignore, underestimate, or misunderstand the value of the evolutionary approach in

understanding the behavioral phenomena they study and that our target article can play an important role in improving communication and exchange of ideas between evolutionary psychologists and other behavioral scientists.

Schein et al. argue that research on attractiveness-related biases cannot determine whether the effects are driven by a positive, beauty-is-good response, as the authors argue, or by a negative, ugly-is-bad response. In reality, there is evidence that beauty-is-good and ugly-is-bad are not independent phenomena and that they both operate simultaneously. For example, research on prostitution has shown that there is a linear relationship between the physical attractiveness of the prostitutes and the amount of money their clients are willing to pay to them. Ugly prostitutes are paid less, and beautiful ones are paid more than the average (reviewed in Hamermesh 2011). Schein et al. write: “Research on ugly-is-bad bias, infant research, and research on same-sex preferences for attractive others are not consistent with most versions of mating strategy” (para. 3). We disagree. Schein et al. reject all evolutionary explanations for attractiveness-related biases and propose, as an alternative explanation a domain general information processing system, cognitive averaging, which results in preferences for attractive faces. First, we emphasize that an explanatory cognitive mechanism is not necessarily alternative to the functional evolutionary explanations we discuss in our target article, because these are explanations at different levels of analyses. Second, although it is true that average-looking faces are generally perceived as attractive, the proposed mechanism, cognitive averaging, cannot explain the phenomenon of attractiveness-related biases for many reasons. One is that these biases are not limited to exposure to faces, but also apply to situations in which (female) attractiveness is measured with waist-to-hip ratios. Another one is that the brain imaging studies we reviewed in our target article indicate that different neural circuits are activated when expressing aesthetic judgments about same-sex beautiful male and female faces and when experiencing mating motivation triggered by beautiful opposite-sex individuals. Finally, objections have been raised by other researchers to the argument that the attractiveness of beautiful faces is entirely accounted for by their prototypicality. For example, in his commentary, **Becker** reviews studies showing that the attention-grabbing properties of beautiful faces cannot be simply reduced to symmetry detection and that memory is more sensitive to beautiful female faces than male faces. He remarks that the morphed prototypical average of attractive female faces is noticeably different from the morphed average of all female faces, suggesting that these faces have additional features for which recognition could be vigilant. Taken together, these findings suggest that attractiveness-related prosocial and financial biases are not triggered by beautiful, average-looking faces in general, but specifically by the beautiful, average-looking faces of potential mating partners, particularly females.

Maguire & Racine’s commentary and their critique of our ideas revolve around a misinterpretation of what we wrote in our target article. They quote a statement we made in section 4.1, paragraph 5, of the target article, which described not our opinions, but the conclusions of a study by Lemay et al. (2010). Many social psychologists assume that stereotypes about attractive individuals cause

people to express favorable behavioral biases toward them. The study by Lemay et al. clearly showed that stereotypes do not play a causal role. People are motivated to affiliate with attractive individuals, and as a result, they construct images of these individuals as interpersonally receptive and responsive. Lemay et al. suggested that people’s stereotypes about attractive individuals, if they ever occur, are a post hoc rationalization of their desire to establish bonds with them. Unlike what Maguire & Racine wrote, our functional explanations for the occurrence of attractiveness-related biases do not imply the existence of a psychological construct about attractiveness or attractive individuals that is in any way similar to a stereotype. We suggest that attractive potential mates grab people’s attention and increase their motivation to affiliate with them the way sexually explicit images grab men’s attention and increase their motivation to view them, or the way the taste of sweet food in the mouth stimulates our appetite for it and increases our motivation to continue ingesting such food. In none of these cases is it necessary or helpful to postulate a psychological construct as an intervening variable mediating our preferences.

We also find it unnecessary to postulate, as **Oda** does in his commentary, that expressing prosocial biases in favor of attractive individuals requires a special imagination or an optimistic delusion that allows people to believe that they can mate with very attractive individuals when the probability of doing so is very low. If prosocial or financial biases in favor of attractive people increase one’s probability of mating with them relative to other individuals who do not express such biases, natural selection will favor any genetically based tendencies to express such biases. To clarify also what we perceive as misunderstandings by other commentators such as **Stephen et al.** and Oda, our account of attractiveness-related biases provides both a functional explanation and a mechanistic explanation for these biases. Our hypothesized perceptual, cognitive, neural, and neuroendocrine mechanisms are different from those implied by stereotype theories and other explanations favored by social psychologists and economists, including the “cognitive averaging” mechanism idea proposed by **Schein et al.** in their commentary.

Unlike what **Stephen et al.** write, some of the brain imagining studies we reviewed, which show activation of neural reward circuitry in response to exposure to attractive faces, are consistent with our hypothesis but not with stereotype theories, because these effects are observed only with faces of potential mating partners (opposite-sex individuals for heterosexuals) and not with the faces of all attractive individuals as predicted by stereotype theories. Clearly, we do not provide a comprehensive account of all mechanisms responsible for attractiveness-related biases. For example, although we acknowledge that social and cultural influences probably contribute to the expression of these biases, we do not examine such influences in our target article. **Renells & Verba**, however, provide an interesting and useful discussion of how social experience acquired during the formative years reinforces the tendency to be positively biased toward attractive faces that is present already in infancy, particularly in the case of attractive female faces.

The contrast between our explanations, which address both function and mechanisms, and those favored by social psychologists and economists, which focus on

mechanisms, does not simply reflect a difference between levels of analyses as suggested by **Oda** and **Ronay & Tybur**. We do not offer a contrast between disciplines that see each other as foes, as noted by Ronay & Tybur. We do not see evolutionary psychology, to use Ronay & Tybur's expression, as the "wolf at the door" that threatens to swallow other behavioral disciplines. We believe that the claims that evolutionary behavioral disciplines will take over the social sciences are unfounded. Evolutionary psychology is no wolf, but social psychology and economics are no lambs either. Ronay & Tybur write that "by themselves, positive stereotypes and taste preferences cannot explain the relationship between attractiveness and prosociality at any fundamental level" (para. 7); however, many social psychologists and economists believe that they do. Although in some cases the explanations provided by evolutionary psychologists are compatible with those of other behavioral scientists, in others they are not. This is the case especially whenever the evolutionary explanations address not only issues of functional significance, but also those of mechanisms, and the hypothesized mechanisms are different than those proposed by other researchers in the same or another discipline. We have already remarked that our evolutionary account of attractiveness-related biases, which addresses both function and mechanism, is compatible with the taste-based discrimination model used by economists. We do believe, however, that the mechanistic explanations of attractiveness-related biases proposed by many social psychologists and economists are substantively different from those proposed in our target article.

The contrast is not between the disciplines but between the specific hypotheses that researchers working within these disciplines have proposed. In our target article, we use the expression "evolutionary explanations" in reference to the three specific evolutionary hypotheses. We agree that they are not the only evolutionary explanations and that future research on attractiveness-related biases should explore other evolutionary aspects of this phenomenon that are not directly related to mate choice but are more broadly relevant to the issue of social partner choice. We are all in favor of researchers from disciplines working together as allies in a common enterprise. Indeed, this is one of the main motives that prompted us to write our target article. We hope that future research on attractiveness-related biases will benefit from the theoretical and methodological tools contributed by different disciplines. We hope that this interdisciplinary research will establish which explanations of attractiveness-related biases are most supported by the empirical evidence, regardless of the discipline from which these hypotheses originated.

R4. Scholarship issues

The authors of two commentaries (**Feingold** and **LaFrance & Eagly**) accuse us of poor scholarship. Feingold describes our article as an old-school qualitative review of the literature and warns that "researchers who conduct qualitative reviews of the attractiveness literature may draw tendentious conclusions that are inconsistent with the findings from past or future meta-analyses" (para. 3). If we wanted to conduct a meta-analysis of the effects of attractiveness on social decision making, we

would have done it and would have written a very different article. Our goal instead was mainly to write an article of ideas, which reviewed the different conceptual perspectives used in previous attractiveness research and critically discussed and integrated the empirical findings of different disciplines. To our knowledge, ours is the first article of this kind to be written about attractiveness research, a field of inquiry in which researchers working within a particular discipline have traditionally ignored, misinterpreted, or dismissed the theoretical and empirical contributions of other disciplines. We hope that our article will generate more comprehensive and integrative research on attractiveness biases, in which the strengths and weaknesses of different disciplinary approaches are recognized. This is an important way in which scientific research advances. Science is not just about *P* values. If conceptual papers are considered "old-school," we are happy to be considered old-school researchers.

As for **Feingold's** criticism that our conclusions contradict those of previous meta-analyses of the literature (e.g., Eagly et al. 1991; Feingold 1992a; Jackson et al. 1995; Mazzella & Feingold 1994), these meta-analyses were conducted more than 20 years ago. Even more recent meta-analyses (e.g., Hosoda et al. 2003; Langlois et al. 2000) are now outdated, given that attractiveness-related biases are an extremely active field of research, with new studies on this topic being published every month. In our target article, we cited approximately 100 articles published after 2000, many of which have provided new empirical data on attractiveness-related biases, and others that have presented conceptual advances that help us better understand this phenomenon. Finally, previous meta-analyses of this literature were selective in that they focused mainly on studies conducted by social psychologists. Studies of the labor market and experimental studies involving economic games were largely ignored. Since 2000, there has been an explosion of studies of the effects of attractiveness on decision making in economics games. These studies using carefully controlled and highly standardized experimental conditions represent an optimal paradigm for investigating attractiveness-related biases. Our review of these studies highlights some clear trends in their results, which make it necessary to re-evaluate the conclusions of previous research and previous reviews of the literature.

We agree with **LaFrance & Eagly** that both men and women value physical attractiveness in their sexual partners very highly, particularly in the context of short-term mating. It is important to remember, however, that most research on the role of attractiveness in mate preferences has focused on people's "ideal" preferences. In the real world, given that women are generally choosier about their sexual partners than are men, it is likely that highly attractive women are less accessible to average-looking men than highly attractive men are accessible to average-looking women. In the labor market and other real-life contexts, this may result in men's biases in favor of attractive women being stronger than women's biases in favor of attractive men. In our target article, we also acknowledged that the stronger attractiveness biases for women than for men in the labor market likely reflect, at least in part, the fact that more men are in positions of power than women and therefore have more opportunities to express their biases. The hypothesis that physical attractiveness is an

indicator of good genes is well accepted by evolutionary biologists, based on evidence from both animal and human research. Whether physical attractiveness is an honest marker of fertility is largely irrelevant to the point in our article. It is well known that for men fertility is generally not an issue, whereas for women the best marker of fertility is age, which explains the universal men's preference for young women.

Contrary to what was stated by **LaFrance & Eagly**, we did not neglect the relation between trustworthiness and attractiveness. In fact, we reviewed studies using experimental trust games, which show that attractive people are trusted more than unattractive ones. That people often infer trustworthiness, dominance, and other traits from faces independent of attractiveness is something we mentioned in our article, but only briefly because it is not strictly relevant to our article, which is focused on attractiveness and not on faces in general. Contrary to what was hypothesized by LaFrance & Eagly, preferences for attractive partners are not a modern human phenomenon. They are widespread in animals as well. It is not astonishing that the overlap in the reference list of our target article and LaFrance & Eagly's commentary is limited to two articles, given that most of the studies they cite are irrelevant to our article. Given that LaFrance & Eagly's commentary does not directly address any of the explanations for attractiveness-related biases we discussed in our article, the statement made in the commentary's title ("Omitted Evidence Undermines Sexual Motives Explanation for Attractiveness Bias") is unwarranted.

R5. Policy implications of research on attractiveness-related biases

Two commentators suggested that the conclusions drawn in our target article, and more generally the findings of research on the determinants of financial and prosocial biases in favor of attractive people, have potentially important implications for society and policy. **Ravina** suggests that "depending on the causes of the positive bias toward attractive people, and the relationship between attractiveness and productivity, prosocial behaviors, and personality traits, we should either ignore the bias or make sure that our employees/decision makers are made aware or protected from it and from the 'mistakes' to which it leads" (para. 7). She also remarks that "understanding the mechanism will also help us identify the people more prone to the bias, the contexts in which it is stronger, and possibly the best devices to protect the decision makers from it when stakes are high, if they do not do so already by themselves" (para. 7).

Similar to **Ravina**, **Minerva** suggests that it is important to conduct research to understand the origins of attractiveness-related biases. She writes: "Although lookism is often considered a politically incorrect topic to discuss, it is only by learning more about it that we will be able to find ways to deal with such a phenomenon and, we hope, alleviate its negative impact" (para. 13). We agree. **Minerva** offers a number of suggestions about how to limit the impact of attractiveness-related biases in the labor market and even suggests that legal measures could be introduced to protect individuals who are penalized by these biases.

We thank both **Ravina** and **Minerva** for their insightful comments and helpful suggestions. Although we did not

discuss any policy implications of the research on attractiveness-related biases reviewed in our target article, we strongly believe that government officials, policy makers, and legal experts should be aware of the results of scientific research on human behavior, especially with respect to how biologically based behavioral tendencies can influence social and economic processes. Nonscientists should also be educated about avoiding the naturalistic fallacy. The fact that some behavioral phenomena have a biological basis and an evolutionary origin in no way implies that they are socially or ethically acceptable or that they are immutable and inevitable. We hope that our target article and the discussion it has already stimulated will generate new knowledge of human behavior, and that this new knowledge will increase our awareness of our biases and give us the tools to control or eliminate them, if we as a society choose to do so.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively]

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