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 Maestripieri 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 comparedwith perceiving nonprototypical stimuli (Leopold et al. 2006; Loffler 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 Maestripieri 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, Maestripieri 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 Maestripieri 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