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Abstract: Evolutionary theories have long been used to generate testable predictions about responses to adult facial cues in the contexts of mate choice, cooperation, and intrasexual competition, among others. More recently, researchers have also used evolutionary theories to guide research on responses to infant facial cues. Here we review some of this work, focusing on research investigating hormonal regulation of responses to infant facial cuteness and the role of kinship cues in perceptions of infant faces. These studies suggest that sex hormones have dissociable effects on the reward value of and perceptual sensitivity to infant facial cuteness. They also suggest that attitudes and behavior towards infants displaying cues of kinship are complex processes influenced by individual differences.

Highlights (3 – 5 bullet points each only 85 chars including spaces)

Evolutionary studies of faces typically analyze adult targets

Infant facial cues are important for adult-child interactions, however

We discuss recent research on hormonal regulation of responses to infant facial cues

We also discuss the role of kinship cues in perceptions of infant faces

Perceiving infant faces

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Perceiving infant faces

Abstract

Evolutionary theories have long been used to generate testable predictions about responses to adult facial cues in the contexts of mate choice, cooperation, and intrasexual competition, among others. More recently, researchers have also used evolutionary theories to guide research on responses to infant facial cues. Here we review some of this work, focusing on research investigating hormonal regulation of responses to infant facial cuteness and the role of kinship cues in perceptions of infant faces. These studies suggest that sex hormones have dissociable effects on the reward value of and perceptual sensitivity to infant facial cuteness. They also suggest that attitudes and behavior towards infants displaying cues of kinship are complex processes influenced by individual differences.

Introduction

Almost all evolutionary research on face perception has focused on adult faces, typically concerning judgments in the contexts of mate choice (i.e., judgments of adults' facial attractiveness), cooperation (i.e., judgments of adults' facial trustworthiness), or intrasexual competition (i.e., judgments of adults' facial dominance). Although there is compelling evidence that infant facial cues are important for adult-child interaction and caretaking [1-3], far less research has examined responses to infant facial cues. This is particularly surprising given evidence that the mechanisms for processing infant and adult faces can be, at least partly, dissociated [4], suggesting that

responses to infant facial cues are not solely a byproduct of mechanisms and processes that evolved primarily for the assessment of adult faces. Here we review evidence from two areas of research on infant facial cues that have been informed by evolutionary theories: hormonal regulation of responses to infant cuteness and the role of kinship cues in perceptions of infant faces.

Hormonal regulation of responses to infant cuteness

Links between sex hormone levels and parental behavior are well established (reviewed in [5]). Since infant facial cuteness also influences parental behavior, such as protection and bonding [1-2], many researchers have hypothesized that sex hormone levels will play some role in the regulation of responses to infant facial cuteness [6-10]. Early results that were presented as evidence for this proposal came from studies reporting that women were better than men at correctly discriminating between high- and low-cuteness versions of infant faces [6,9] (Figure 1). Sprengelmeyer et al. [9] also reported that women using hormonal contraceptives performed better on this cuteness discrimination task than did women not using hormonal contraceptives and that pre-menopausal women performed better than did post-menopausal women. While these between-group differences in performance on infant cuteness discrimination tasks are consistent with the proposal that hormones contribute to the regulation of responses to infant facial cuteness, there may be other differences between the groups that could explain differences in task performance (see, e.g., [11] and [12] for other sources of differences in responses to infant facial cues). Other studies also suggest that these between-group differences in cuteness discrimination may

not be robust. For example, some studies have reported similar performance on infant cuteness discrimination tasks in women using and not using hormonal contraceptives [10] and in men and women (e.g., [13]). These latter results are consistent with other research reporting that men and women show similar behavioral, neural, and perceptual responses to infant faces [14-16].



Figure 1. An image of an infant face with increased (left) and decreased (right) perceived cuteness.

While the studies described above tested for evidence of hormonal regulation of responses to infant facial cuteness using between-groups comparisons, more recent studies investigating this issue have focused on within-person comparisons. Lobmaier et al. [7] reported that women's (N=29) performance on an infant facial cuteness discrimination task similar to those used in previous studies was better when they were tested during the ovulatory phase of their menstrual cycle than when the same women were tested during the mid-luteal cycle phase. Since performance on the infant cuteness

discrimination task did not covary with measured salivary estradiol, progesterone or testosterone, they speculated that oxytocin and/or prolactin regulates cuteness discrimination in women. Although Sprengelmeyer et al. [10] observed no evidence for an effect of cycle phase on women's responses to infant facial cuteness using images that varied naturally in cuteness, we suggest that this null result be treated cautiously, given the relatively low number of women tested (N=11).

Hahn et al. [17] also tested for evidence of hormonal regulation of women's (N=60) responses to infant facial cuteness using a longitudinal design. Like Lobmaier et al.[7], they also found no evidence that changes in women's performance on an infant facial cuteness discrimination task were related to their salivary estradiol, progesterone, or testosterone. Consistent with other studies of women's responses to infant facial cuteness [16,18-20], analyses of the same women's responses on a widely used behavioral measure of stimulus reward value (a standard lever-press task, [21]) showed that women were willing to expend more effort to view images of infant faces in which cuteness had been increased than they were to view images of infant faces in which cuteness had been decreased. Moreover, this effect of cuteness on the reward value of infant faces was greatest when women's measured salivary testosterone levels, but not estradiol or progesterone levels, were high. Finally, they demonstrated that the tendency for the reward value of infant facial cuteness to track changes in women's testosterone levels was independent of the possible effects of changes in cuteness ratings. These results are consistent with previous work showing that administering

testosterone to women increases the reward value of infant vocalizations [22] and suggest that testosterone may regulate the reward value of infant facial cuteness, at least to women. Given cuter infants tend to both be healthier [23] and be perceived to be healthier [24], increased motivation to approach cute infants when testosterone is high could reflect increased selectivity in preferences for caring for healthy infants when competition for resources is more intense.

Together, Hahn et al's [17] and Lobmaier et al's [7] findings suggest that different hormonal mechanisms independently contribute to the regulation of two dissociable aspects of women's responses to infant facial cuteness: discrimination and reward. Further work is needed to clarify how robust these effects are and the functions of these within-woman changes in responses. For example, it is unclear whether these effects are specific to infant facial cues or simply further evidence for hormonal regulation of responses that have been observed in other domains (e.g., responses to adult facial attractiveness or monetary rewards, [25,26]). While research on the possible hormonal regulation of responses to infant facial cuteness has focused on women's responses, investigating men's responses might clarify the role hormones play in shaping responses to infant faces.

The studies of infant facial cues discussed so far investigated responses to infant facial characteristics that people respond to positively *on average* (perceived cuteness). By contrast, other work investigated responses to aspects of infant facial appearance that are more idiosyncratic (kinship cues).

The role of kinship cues in the perception of infant faces

While research on the hormonal regulation of perception of infant facial cuteness generally focuses on women's perceptions, research on perceptions of family resemblance in infant faces generally focuses on men's perceptions. The allocation of parental investment can have serious consequences for one's genetic fitness. Thus, biologists expect there to have been strong selection for discriminating genetically related from unrelated children. Because of the physiology of mammalian reproduction, maternity is almost never in doubt, while paternity can be in question. Here, we will focus on two hypotheses about infant family resemblance: (1) Do babies look more like their fathers than their mothers? and (2) Do men respond to infant facial resemblance differently than women do?

Advertising paternity through phenotypic cues such as facial resemblance can result in both benefits and costs to infants. For example, perceived paternal resemblance predicts men's financial investment in children [27,28]. However, non-paternity can lead to loss of paternal resources [29] or even neglect, abuse and infanticide [30]. Theoretical assessments of the costs and benefits of advertising paternity have come to mixed conclusions, with some suggesting that moderate non-paternity rates should select for infants who do not signal their paternity [31,32], and others suggesting that higher rates of non-paternity will select for infants who actively resemble their fathers [33]. While mistaken paternity is rare (~2%) among men who have high paternity confidence [34,35], this figure ranged from 0.4% to 11.8% across the 22

groups studied by Anderson [34], which included both preindustrialised groups (e.g., Yanomamo) and postindustrialised groups (e.g., France). Additionally, among men with low paternity confidence who requested paternity testing from a laboratory, 14.3% to 55.6% of these men were correct in their doubt [34].

So *do* babies actually resemble their fathers more than their mothers? One high-profile study showed that people could match a sample of 24 one-year-olds to their fathers more accurately than to their mothers [36], although this bias disappeared by age ten. However, multiple higher-powered studies using better-controlled images have not replicated this finding [37-41].

Despite very little evidence that babies preferentially resemble their fathers, people certainly do report seeing a stronger resemblance between newborns and their fathers than between newborns and their mothers. In studies conducted in Canada [42], Mexico [43] and the United States [40], newborns' resemblance is ascribed to their fathers significantly more than to their mothers, at least by mothers and their families. Indeed, beliefs about relatedness, even when inaccurate, have been shown to powerfully bias perceived parental resemblance [44].

Given the evidence and theory, it seems unlikely that humans have been selected to overtly advertise their paternity, at least through facial resemblance. However, because parental uncertainty is greater for men than women, selection on perceptions of or responses to family resemblance in

putative children may have been stronger in men than women. One method for investigating this question has been to assess men's and women's responses to images of children whose faces have been made to resemble their own through computer graphics. Some research using this method has found consistent sex differences, where men are more willing to adopt or invest in self-resembling infants than women are [45,46]. However, others have argued that the methods used in this research created confounds that could have accounted for this sex difference [47]. For example, the foil faces were made from both male and female adult faces, so that an overall bias towards boy's faces would have resulted in a bias towards self-resemblance for men and a bias away from self-resemblance for women. Further work eliminating such confounds from the experimental design has either shown no sex difference in attitudes towards self-resembling infants [47] or a sex difference in the opposite direction [48].

One potential reason for these diverse findings is that there are individual differences in the effects of self-resemblance on attitudes towards self-resembling infants. Welling, Burriss and Puts [49] tested preferences for self-resembling and partner-resembling infant faces in 67 heterosexual couples. While both men and women preferred self-resembling infant faces, neither had a significant preference for partner-resembling infant faces. Additionally, men's mate retention tactics were significantly correlated with their preferences for self-resembling infant faces—men who scored higher on measures of mate guarding behaviors directed towards their partner (intersexual manipulations) also had greater preferences for self-resembling

infants [49]. Women's mate retention tactics were not associated with their preferences for self-resembling faces. This work can potentially reconcile the inconsistent sex differences in the previous literature. While all of this research found that women showed small, but significant, preferences for self-resembling infants, they differed in whether men's preferences for self-resembling infants were larger [45,46], not significantly different [47] or smaller [48]. These findings may, then, reflect group or cultural differences in men's perceived need for mate retention behaviors.

Recently, researchers have begun to seek neural correlates of potential sex differences in the perception of self-resemblance in infant faces. While behavioral work has found little evidence of sex differences in the ability to detect family resemblance to self or others [46,47,50], some studies have reported sex differences in the brain areas activated by self-resemblance (e.g., [51,52]). More recently, Wu and colleagues [53] combined behavioral and electrophysiological (ERP) techniques to investigate the detectability of computer-graphic manipulated self-resemblance in adult and child faces. While men and women were equally good at detecting self-resemblance in adult faces, men were significantly better at detecting self-resemblance in child faces. Additionally, men showed a smaller N2 component in the anterior cingulate cortex (similar to effects previously found for own face) for both adult and child self-resembling faces.

When considered together, the theoretical work on conditions under which paternity advertisement might evolve, the findings for actual resemblance

between parents and infants, the findings for biased perception of resemblance, and findings for attitudes and behavior towards self-resemblance in infants points to a complex process that is likely to be heavily influenced by individual differences. We suggest a Bayesian approach to integrating kinship cues [54] will be a fruitful approach to further investigating potential sex differences in perceptions of and responses to self-resemblance in infant faces.

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testosterone levels were high. There were no corresponding effects of estradiol or progesterone and no effects of sex hormones on women's perceptual ratings of the infant faces' cuteness. That women's testosterone levels appear to regulate the reward value of infant facial cuteness in this way is consistent with work in which administering testosterone to women increased the reward value of infant vocalizations (Bos et al., 2010).

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