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Mate Preferences Across the Lifespan

Lynda G. Boothroyd & Jovana Vukovic

Abstract: Humans show preferential responses to 'attractive' individuals from the first hours of life onwards. However, these early preferences are subject to later development, both in terms of increasing agreement on general attractiveness, and the emergence of preferences for specific dimensions of attractiveness relevant to mate choice. Here we firstly outline key aspects of mate choice and consider evidence for their hormonal mediation in adults of reproductive age. We then examine preferences for these traits across key periods of hormonal changes, namely: infancy, puberty, and menopause; and consider potential hormonal mediation arguments for the mate choice changes observed during these periods. We find overall that expression of specific preferences is ambiguous in infancy, but there is clear evidence that preferences become stronger in late childhood and adolescence (albeit subject to disruption around puberty). There is also a modest evidence base suggesting a decline in some preferences at menopause in women. Across the developmental and lifespan literature, however, there is a critical lack of studies assessing hormones directly. We close with key recommendations for future research.

Keywords: facial attraction, voices, waist-hip ratio, sexual dimorphism, symmetry, averageness, health, dehydroepiandrosterone, testosterone, estradiol, progesterone, infancy, adrenarche, puberty, menopause

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Mate choice lies at the core of evolutionary understandings of human behavior. Given that selection of a mate, versus random mating, can yield increased reproductive success even in *Drosophila* (Edward & Chapman, 2012), it is unsurprising that a long-lived species with high levels of parental investment, such as humans, demonstrates high levels of choosiness with regards to sexual partners. Furthermore, although males may on average invest less than females, high rates of pair-bonding, (serial) monogamy, and male provisioning of offspring lead to the prediction that humans should display mutual mate choice (Brown, Laland & Mulder, 2009; Kokko & Johnstone, 2002; Stewart-Williams & Thomas, 2013), with males and females both seeking to detect and select partners on the basis of traits that will maximize immediate reproductive success and/or long-term inclusive fitness.

Although initially most developmental research into attraction assessed the extent to which different age groups 'agreed' in their overall preferences for some faces over others, in the last ten years, researchers have built a body of data that considers developmental change in preferences for specific traits. Theories around the traits that humans tend to find attractive in potential reproductive partners focus on the immediate benefits to the chooser, the longer term indirect benefits to offspring, or both. Below, we outline the principle understandings of the benefits derived from those traits that have been investigated in developmental/lifespan contexts thus far, and the methods used to assess preferences for these traits. Next, we go on to consider critical developmental windows in which hormonal changes may impact preferences: namely, infancy, puberty, and menopause.

Traits typically preferred by adults

Direct indices of current health in a potential partner may include elements of vocal quality (e.g., Orlikoff, 1990), levels of carotenoid-linked yellow coloration in the skin (e.g., Stephen, Coetzee, & Perrett, 2011), and the overall visible health of the face and skin quality (e.g., Fink & Matts, 2008; Jones et al., 2001). Selection of a more currently-healthy mate yields potential reproductive benefits in terms of increased individual fitness via contagion avoidance, and increased inclusive fitness via (potentially) elevated offspring health (although see Adamo & Spiteri, 2009, for discussion of this point). To date, although the adult literature is increasingly interested in the specific skin and voice properties associated with health, the developmental literature has investigated only global facial health as determined by third party observers; Boothroyd, Meins, Vukovic and Burt (2014) constructed pairs of stimuli varying in skin color, texture, and face shape, based on composites of individuals rated as appearing very healthy or very unhealthy and found that children preferred the

'healthier' faces from 6 to 8 years onwards. Relatedly, Kościński (2011, 2013) had child participants rate the attractiveness of individual faces already rated by others for a healthy appearance and found a positive correlation between child-perceived attractiveness and adult-perceived health.

Symmetry and averageness are often considered to be indices of underlying quality with significant implications for health (reviewed in, e.g., Stephen & Wei, 2015). Although the literature regarding symmetry presents an overall only modest link to health (Van Dongen & Gangestad, 2011), individuals may yet benefit by selecting more symmetrical partners if the factors that lead to their elevated levels of symmetry result in more viable offspring. Similarly, there is evidence that men with more diverse Major Histocompatibility Complex (MHC) alleles, who may be resistant to more pathogens, have more 'average' faces than men with less diverse genetic profiles (Lie, Rhodes & Simmons, 2008). Thus, averageness may offer comparable potential benefits to offspring as symmetrical traits do.

Symmetry can be quantified based on the deviations away from perfect bilateral symmetry (e.g., bodies: Gangestad, Thornhill & Yeo, 1994; faces: Penton-Voak et al., 2001); it is important, however, to exclude systematic asymmetries, where all individuals tend to show asymmetry in one direction (directional asymmetries, e.g., the heart is situated asymmetrically to the left of midline) or in either direction (anti-symmetry, e.g., handedness). The remaining 'random' asymmetries are known as fluctuating asymmetry. Although some studies of associations between body asymmetries and health or mating outcomes do control for systematic asymmetry (e.g., the body landmarks chosen by Gangestad et al., 1994, are not typically subject to directional asymmetries), most studies of attraction simply look at preferences for stimuli varying in naturally occurring asymmetries without isolating fluctuating asymmetry specifically. For instance, the developmental studies of symmetry preference discussed here all presented pairs of stimuli in which the natural asymmetries of an individual had been reduced/eliminated, or left intact, or even exaggerated.

Averageness is considered almost exclusively in reference to faces (indeed we are unaware of any studies looking at other forms of averageness), and refers to the degree to which the proportions of an individual face resemble the population mean for those proportions. Preferences for averageness can be determined by correlating attractiveness ratings of individual faces with composite averageness scores for those faces. The majority of research in developmental contexts, however, tends to manipulate the proportions of individual facial identities to make them closer to population average (usually based on the proportions of 25+ individuals drawn from the same recruitment pool) and to exaggerate the differences between the faces and the average (i.e., to make them more distinctive; see, e.g., Boothroyd et al., 2014; Griffey & Little, 2014).

Sexual dimorphism, in the context of attraction research, refers to the degree to which an individual demonstrates sexually dimorphic features – i.e., how strongly they show sex-typical shape, color, or size. In terms of body size and shape, there has been a great deal of research into preferences for female waist-hip ratio, which is lower (i.e., more curvy) in women than in men, and for dimensions relating to shoulder or chest width in men (e.g., waist-shoulder and waist-chest ratio, respectively; reviewed in Reeve, Kelly, & Welling, 2016). Facial shape is also sexually dimorphic and is the focus of a vast research literature considering preferences for femininity in female faces and women's ambiguous attitudes towards masculinity in male faces (reviewed in Little, 2015). Finally, voice pitch is also sexually dimorphic, being deeper in men. Various researchers have linked sexual dimorphism in the female direction (i.e., femininity) with estrogen (e.g., Law Smith et al., 2006), whereas dimorphism in the male direction (i.e., masculinity) has been both correlational (e.g., Pound, Penton-Voak & SurrIDGE, 2009) and pseudo-experimentally linked (e.g., Verdonck, Gaethofs, Carels & de Zegher, 1999) to testosterone. Femininity is hypothesized to confer advantages in terms of fertility, such that males selecting more feminine female partners may be more likely to sire offspring during a given sexual encounter. Masculinity in men is more controversial and has been hypothesized to indicate underlying quality and to yield health benefits to offspring (e.g., Thornhill & Gangestad, 2006; although see Scott, Clark, Boothroyd & Penton-Voak, 2013, for a counter-argument, and Boothroyd et al., 2017, for recent counter-evidence). Alternatively, masculinity may be primarily a signal of intra-sexual competitiveness (Boothroyd, Jones, Burt & Perrett, 2007; Puts, 2010). In either case, men who have more feminine faces are thought to be warmer, more cooperative, and more suitable long-term partners (Boothroyd et al., 2007; Perrett et al., 1998), while higher pitched (i.e., more feminine) voices are likewise perceived as less dominant (Puts, Hodges, Cardenas & Gaulin, 2007). The bulk of the developmental literature into facial preferences has tended to utilize stimuli in which femininity is the preferred direction amongst the oldest participants, for both male and female images (e.g., Boothroyd et al., 2014; Saxton et al., 2009, 2010). As such, in

this context, the question is primarily the extent to which children demonstrate adult-like preferences for femininity. Similarly, where we report on voice preferences, we will focus on whether the preferences exhibited are 'adult-like' or not, regardless of direction. The only research to investigate body preferences from a developmental angle focused on children's emerging preferences for differentiated waist-hip ratio between male and female silhouettes (Connolly, Slaughter & Mealey, 2004).

Evidence for hormonal associations in adults

To our knowledge, these traits above are the only widely recognized specific preferences that have been investigated from a developmental perspective, although Kościński (2010, 2011, 2013) has also considered the extent to which children prefer faces that adults have rated on other non-physical characteristics (e.g., friendliness, sexy appearance). Preferences for the facial, vocal, and body traits discussed above have also been the focus of research into endocrine influences on mate choice among adults of reproductive age. Expression of female preferences for multiple forms of male masculinity across the menstrual cycle may be driven by both estrogen (Feinberg et al., 2006; Roney & Simmons, 2008; Roney, Simmons & Gray, 2011; Pisanski et al., 2014; although cf Dixon et al., 2018 and Jones et al., 2018) and testosterone (Bobst et al., 2014; Thornhill, Chapman & Gangestad, 2013; Welling et al., 2007, although see Roney et al., 2011), with a potential effect of progesterone in suppressing masculinity preferences (Jones et al., 2005b; Limoncin et al., 2015; Little, Burriss, Petrie, Jones & Roberts, 2013; but see Cobey, Little & Roberts, 2015; see also Welling & Burriss, this volume). Similarly, within-subject variation in men's preferences for female femininity is associated with testosterone (Welling et al., 2008; see also Bird et al., 2016).

On the other hand, female preference for male healthiness may be driven by progesterone insofar as women prefer healthiness more in a potential partner during the luteal phase of the cycle than the follicular phase, when taking hormonal contraceptives (which contain artificial progestins) than when naturally cycling, and when pregnant than when not pregnant (Jones et al., 2005a,b). There is also a hint that hormones may play a role in symmetry preference; although variation in symmetry preferences across the cycle is subject to limited and conflicting evidence (Gangestad & Thornhill, 2008; Gildersleeve et al., 2014), Hadza women prefer more symmetric male faces when pregnant or lactating than when naturally cycling (Little, Apicella, & Marlowe, 2007). Pregnancy and lactation are hormonally distinct periods, however, and the authors do not give their data separately. Furthermore, Cobey et al., (2015) found that women's masculinity preferences differed between pregnant and post-natal participants, suggesting these periods may also show differences in other trait preferences. As such, it is not clear whether any particular hormone is driving this pattern. Finally, an elevation in symmetry preferences would be surprising during a period in which normal female sex hormones are suppressed, as they are in lactation in particular.

Overall, therefore, there is strong reason to believe that hormonal factors may drive the expression of mate preferences in adulthood, particularly for masculinity/femininity and health, and may thus have a role to play in developmental change in mate preferences.

Facial preferences in infancy

The first step in understanding the development of mate preferences is to consider how early the preferences described above can be observed. Within the first few hours of life, infants show preferences (as indexed by looking times) for some faces over others, in a manner which is consistent with adult judgements of overall attractiveness. For instance, Slater et al. (1998, 2000) have shown that neonates spend longer looking at female faces that adults have rated as attractive compared to female faces rated as unattractive. Furthermore, re-analyzing all the infant-level data presented by Slater et al. across both papers shows that age in hours (which ranges from 7 to 174 hours) does not relate to the strength of infants' preferences for the 'attractive' faces ($r_{50}=0.195$, $p=0.18$), which suggests that either the preference is formed within the first six hours of life and remains stable thereafter, or that infants are born with a basic representation of attractiveness.

Some authors, such as Langlois, Roggman and Musselman (1994), have argued that averageness is the core feature underlying general attractiveness in adult faces, and Rubenstein, Kalakanis and Langlois (1999) have suggested that since neonates may see 16+ faces within hours of birth, we might expect an early facial preference for averageness. Specifically, they argued that infants may rapidly construct a prototype of faces within the local population and utilize this prototype in coding individual faces, with faces closer to the prototype (i.e., more average) being easier to process and thus favored. There is evidence for norm-based coding of facial identity and

attractiveness in adults' preferences (e.g., Rhodes et al., 2003), and there is also evidence that stimuli that are easier to process trigger more positive affect than those that are harder to process (Winkielman, Halberstadt, Fazendeiro & Catty, 2006). Indeed, this is one hypothesis behind why infants prefer female faces in general: that they have greater experience with female faces and find them easier to process (for discussion see, e.g., Ramsey-Rennels & Langlois, 2006). However, crucially, de Haan, Johnson, Maurer and Perrett (2001) found that the ability to form facial prototypes begins at approximately 2 months of age and that early preference must instead have an alternative basis. Although three-month-old infants treated a composite of previously seen faces as 'familiar' (e.g., by attending more to a completely novel face), one-month-old infants did not show this pattern. These data therefore support Slater et al.'s suggestion that although later experience may revise our internal prototypes, humans must have an innate, simple face-representation against which neonates may code novel faces.

Research into the specific components of facial attractiveness that infants favor is relatively sparse. Although Rubenstein et al. (1999) found infants preferred a composite (i.e., average) face comprised of 32 individual faces to an unattractive face in a paired visual preference test, this is difficult to interpret as we know that composite faces are of *at least* average attractiveness, and often (but not always) more attractive than the individual faces used (see Perrett, May & Yoshikawa, 1994, for early evidence regarding attractiveness beyond simple averaging). A more appropriate test of this hypothesis is to compare stimuli in which individual faces have been manipulated to be closer to population average in facial structure (i.e., more average) or further from it (i.e., more distinctive). Using this method, Rhodes et al. (2002) found that six-month-old infants had a potential preference (indexed by length of 'longest look' in each trial, as coded by human observers; there was no difference in overall looking times) for *less* average/more distinctive faces. Similarly, Griffey and Little (2014) used computer-mounted eye-tracking and found that sixty-four 12- to 24-month-olds likewise had a significant visual preference for more distinctive, over more average, faces in terms of overall looking time.

Both Rhodes et al. (2002), and Griffey and Little (2014) also investigated preferences for symmetry in faces, and found contrasting results; Griffey and Little's toddlers showed a significant visual preference for symmetric over asymmetric faces, whereas Rhodes et al.'s infants showed a longest look fixation that tended towards asymmetric faces. Other research found no evidence for symmetry preferences in infants (Samuels et al., 1994), although the stimuli used in this research failed to show a symmetry preference in adults either, which is highly unusual in the wider literature (reviewed in Little, 2015) and likely reflects a deliberate decision by the authors to present naturally varying more and less symmetric faces from different individuals in pairs matched to be overall equally attractive.

There are two key caveats to be addressed in terms of infant preferences for symmetry and averageness; firstly, although averageness may be attractive beyond any elements of symmetry (as discussed by, e.g., Rubenstein et al., 1999), it is not clear whether previous research into infant preferences has controlled for the fact that average faces are also more symmetrical than individual/less average faces. Secondly, most research thus far appears to have concentrated on female faces. Although infants undoubtedly process female faces more efficiently and at a younger age than male faces (see, e.g., Ramsey-Rennels & Langlois, 2006), it is nevertheless important to consider infants' preferences for these traits amongst male faces, not least because approximately half of infants will go on to use male facial features as the basis for choosing a mate.

Research into preferences for sex-typicality (i.e., masculinity and femininity) is likewise sparse. Early data suggested that infants show preferences for larger eyes (Geldart, Maurer & Carney, 1999) and more 'baby-like' adult features (Kramer, Zebrowitz, San Giovanni & Sherak, 1995), which are both contributors to a feminine appearance (Boothroyd et al., 2005). Only two studies have specifically investigated sexual dimorphism. Rennels et al. (2016) found no visual preference for either high- or low-masculinity in naturally varying male faces amongst forty 6- and 12-month-olds. Contrastingly, Griffey and Little (2014) found a significant visual preference amongst their 12- to 24-month-olds for manipulated femininity in both male and female faces. The advantage to Griffey and Little's data is again the use of eye tracking rather than human coding of looking times, although Rennels et al.'s coders showed high inter-rater reliability. Another difference between the studies is the use of stimuli in which faces were fully masked (i.e., hair and clothing covered; Griffey & Little, 2014) versus covering clothing only (Rennels et al., 2016). Adult data may suggest that preferences for femininity should be stronger in the masked stimuli (DeBruine, Jones, Smith & Little, 2010), although in pilot data with children, Boothroyd et al. (2014) found a nonsignificant trend whereby facial

preferences were stronger using unmasked stimuli. Perhaps most crucially, Rennels et al. (2016) used pairs of faces that varied in masculinity but that were matched in attractiveness (as rated by adult observers), which means direct comparison with objectively manipulated masculinity (as per Griffey & Little, 2014, and a large portion of the adult literature) is challenging. One key finding in Rennels et al.'s study, however, is that infants may find highly masculine male faces more challenging to process (as indexed by categorization performance) unless those faces are also high in attractiveness; these findings are consistent with the idea that female faces may predominate in infants' facial experience and should therefore predict a tendency to favor femininity in male faces, which perceptually makes them more similar to the female average (although it does not explain why infants would prefer exaggerated femininity in female faces).

Overall, studies of face preferences in infants suggest that there are demonstrable early preferences for neoteny/femininity, for female faces over male faces, and for distinctive rather than average faces. Preferences for symmetry remain less clear, although the strongest study to date (Griffey & Little, 2014) found a preference for symmetry in late infancy. These data are challenging to integrate. Sex hormones are high in early infancy, but a simple model of hormone levels driving more strongly expressed preferences, as per the adult literature, is clearly inadequate here. Preferences for neoteny/femininity and even symmetry (if such a preference exists) can potentially be explained by visual experience, although preferences for distinctive over average faces defy that explanation. Early sex hormones, however, are often described as 'organizational' and thus, once the limitations in infant visual perception are taken into account, may not direct attention to adult-preferred traits. Furthermore, visual preference itself is problematic as a direct proxy for affective preference; visual attention during early development may serve multiple learning purposes without necessarily indicating social preference. All of these early tendencies are also subject to change across childhood and it is in this latter window (and puberty especially) that activational hormonal effects may be more pertinent (the Organizational-Activational hypothesis is further discussed in Hampson, this volume).

Activation of preferences across childhood and puberty

Although there is evidence that children continue to broadly agree with adults regarding the faces they consider attractive once they are able to verbally report preferences for naturally varying stimuli (e.g., Boothroyd et al., 2014; Cavior & Lombardi, 1973; Cross & Cross, 1971; Kissler & Bauml, 2000; Saxton, Caryl & Roberts, 2006), data on specific trait preferences remains sparse for the pre-pubertal period. To our knowledge, four studies have examined a cross-section of children on specific aspects of traits that contribute to mate preferences in adults. Connolly et al. (2004) found that although there was a general trend for children aged 6 to 15 years to increasingly view male and female body shapes as distinct with age, they only began to significantly distinguish between male and female waist-hip ratios around 10 to 12 years of age. Similarly, Boothroyd et al. (2014) showed children aged 4 to 17 years pairs of faces manipulated in averageness, symmetry, femininity, and healthiness; facial healthiness was significantly preferred over unhealthiness from age 6 to 8 onwards, and symmetry and averageness were significantly preferred from 9 years onwards. Femininity was not preferred until 17 years (although some authors have found femininity preferences in peri-pubertal groups; see below). Vingilis-Jaremko and Maurer compared 5-year-olds, 9-year-olds, and adults on preferences for symmetry and averageness; like Boothroyd et al., they did not find evidence for symmetry preferences until 9 years of age (Vingilis-Jaremko & Maurer, 2013a); they did however find averageness preferences from 5 years of age onwards (Vingilis-Jaremko & Maurer, 2013b). In both cases, preferences became stronger between 5 and 9 years, and between 9 years and adulthood. It is useful to note that Boothroyd et al. used adult stimuli, whereas Vingilis-Jaremko and Maurer used stimuli drawn from each of their three participant age groups, and found corresponding patterns of preference in each.

The pattern of results observed in infants by Rhodes et al. (2002), and particularly Griffey and Little (2014), strongly suggests that the lack of preferences seen in Boothroyd et al.'s 4- to 5-year-olds for all traits, and Vingilis-Jaremko and Maurer's (2013a) 5-year-olds for symmetry, is not due to an inability to perceive the differences between manipulated stimuli. Rather, it seems that from infancy onwards, differences between symmetric and asymmetric, and average and distinctive versions of the same faces can be visually distinguished, but preferences for specific characteristics such as these may only emerge (or re-emerge) in later childhood. This point further highlights the fact that maturation of the visual system alone is unlikely to explain the onset of preferences for specific facial characteristics.

A larger literature exists examining preferences during puberty. Multiple studies have found evidence for symmetry, averageness, health, and femininity preferences existing from 11 or 12 years onwards (Boothroyd et al., 2014; Kościński, 2011, 2013; Saxton et al., 2009, 2010, 2011), although Little et al. (2010) found a significant preference for masculinized male faces in 11- to 14-year-old girls. Where these studies have utilized adult comparison samples, results have tended to show that although specific preferences have been activated by puberty, they are still not expressed at adult levels until some point after age 14 (e.g., Boothroyd et al., 2014; Vingilis-Jaremko & Maurer, 2013a,b). Similarly, Saxton et al. (2006) have found that the nature of adolescents' voice and face preferences show more agreement than those of younger groups, but still do not show full agreement with adults' ratings of the same stimuli. Furthermore, Saxton et al. (2010) found no evidence of 12- to 14-year old participants showing preferences for masculinized or feminized voice pitch.

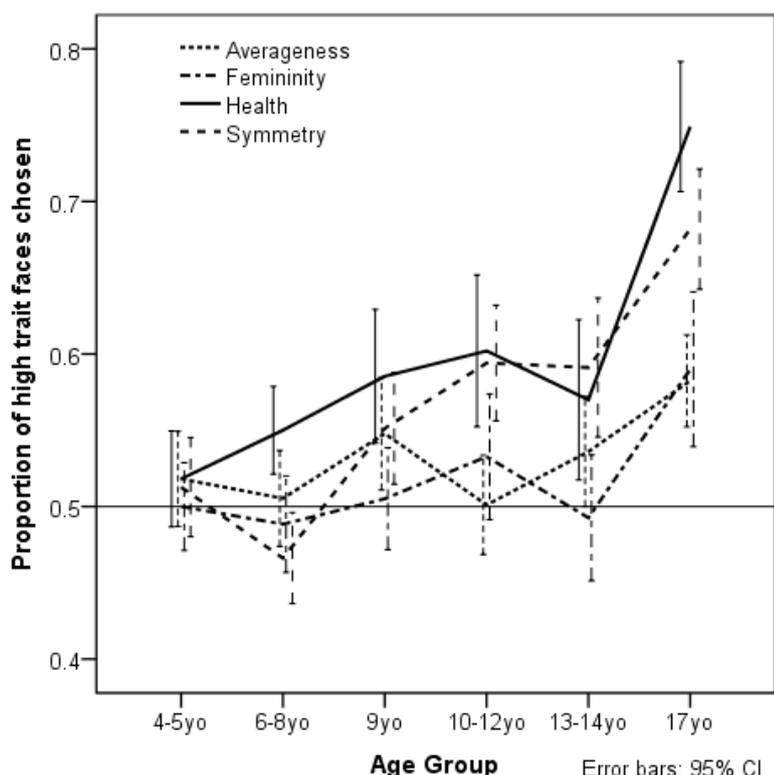


Fig. 1. Summary of the trajectories of specific face preferences with age (data from Boothroyd et al., 2014). Most traits show stronger preferences across mid-childhood, with a dip or plateau around puberty, before increasing to adult levels by 17 years.

Children were grouped by putative dehydroepiandrosterone (DHEA) levels/puberty stage; 4-5 DHEA at floor, 6-8 early adrenarche, 9 later adrenarche, 10-12 late adrenarche/early gonadarche, 13-14 late gonadarche, 17 years adult-like hormones.

Documenting and explaining the actual changes that occur during puberty, however, is a more challenging question. The first study to attempt comparison of different peri-pubertal groups found that 13- to 14-year-olds had stronger facial preferences than 11-year-olds (Saxton et al., 2009), a finding that was replicated in a study comparing 11- to 13- and 14- to 15-year-olds (although there were fewer age differences in preferences for female than male faces; Saxton et al., 2011). However, another study from the same authors suggested that these group differences may have been the result of using different, age-matched stimuli for each age group. When two age groups were tested with matching stimuli, no main effect of age on face preferences was found (Saxton et al., 2010). In fact, although overall means for femininity and symmetry preferences increased with age, preferences for averageness decreased. Correspondingly, Kościński (2010, 2011, 2013) found a similar pattern of means in strength of preference for skin health in girls and boys aged between 11 and 14 years. In the only longitudinal data on facial preferences we are aware of, Saxton et al. (2011) were unable to document any clear changes in adolescent's facial preferences over a 1 year period, although in a later study on voices it was observed that 11- and 13-year olds showed a drop in voice pitch preference over a 9-12 month period (Saxton et al., 2013; see also Saxton et al., 2009 for similar cross-sectional patterns in voice pitch preference). These results are concordant with Boothroyd et al.'s (2014) cross-sectional data shown in Figure 1. Preferences for health, symmetry, and averageness all emerged in mid-childhood, but showed a plateau or dip sometime between 10- and 14-years of age before increasing to adult levels by age 17. Likewise, although directional preferences for femininity never exceeded chance levels until age 17, the same pattern of a drop in preferences occurred at 13-14 years.

There are therefore two issues that need resolving when considering preferences across childhood and adolescence: (1) what causes these preferences to emerge in the first place? And (2) why, when we would expect an explosion in mate-choice relevant behavior at puberty, do we instead see this emergence disrupted? In explaining the emergence of specific preferences across childhood, one hormone has come under repeated speculation. The earliest stage of puberty is adrenarche, when the adrenal gland primes the body for full puberty by releasing dehydroepiandrosterone (DHEA), a hormone that mainly acts as a precursor to other sex hormones. DHEA release begins around 6 years of age and increases dramatically around 9 to 11 years (de Peretti & Forest, 1976; see Figure 2). This surge in DHEA may trigger the first conscious feelings of sexual attraction in boys and girls (McClintock & Herdt, 1996). Furthermore, levels of DHEA are also high during the post-natal period, but drop to floor by age 2. If DHEA plays a role in the development of specific mate preferences, this may explain the apparent U-shaped curve in certain facial preferences across infancy and early childhood; as such DHEA is an obvious candidate hormone for activation of adult-like preferences for specific facial traits, as has been suggested by multiple authors (e.g., Boothroyd et al., 2014; Connolly et al., 2004; Saxton et al., 2009).

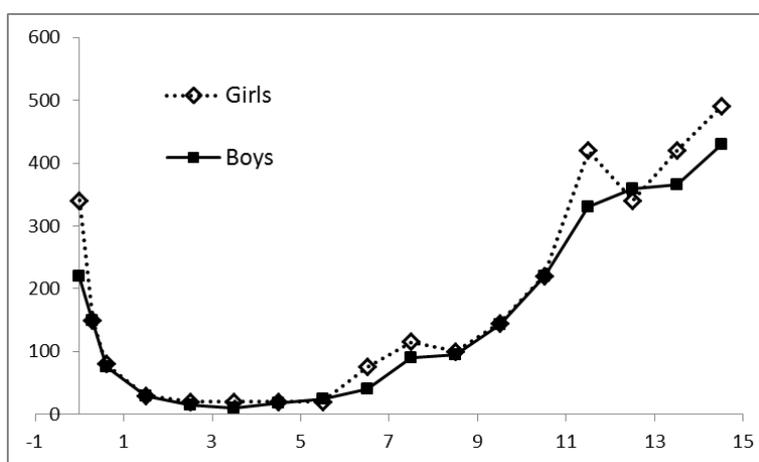


Fig. 2. DHEA levels (ng/100 ml) across 0-15 years, re-drawn from de Perretti & Forest (1976).

With respect to facial preferences in particular, it is useful to consider the wider literature on the development of face processing. A cognitive approach to facial preferences assumes that preferences at least partially reflect the manner in which faces are processed and stored in the brain. Thus, children's judgements of attractiveness may become more similar to those of adults as they get older because of increasing expertise in the perceptual and processing skills required to evaluate aspects of attractiveness. Research has not yet investigated links between children's facial preferences and their processing of other visual stimuli; furthermore it has been argued that face processing is essentially mature by mid-childhood (McKone et al., 2009, 2012; but see Susilo, Germine & Duchaine, 2013). However, much like the pattern of face preferences plateauing during later puberty, a 'developmental dip' in other forms of facial processing occurs around the same age. Multiple studies have documented a period between 10 and 14 years of age in which performance on face recognition either dips or plateaus before increasing to adult levels later on (Carey, Diamond, & Woods, 1980; Chung & Thomson, 1995; Lawrence et al., 2008). Recent evidence has shown that the dip is specific to processing faces; Johnston et al. (2011) found that both facial identity recognition and facial emotion recognition showed a dip, but that recognition of other complex stimuli, namely butterflies, did not. These data rule out alternative explanations such as task-demands affecting performance and suggest that the 'dip' is specific to facial (and perhaps particularly social) stimuli.

This developmental dip in face processing has been hypothesized to be part of a broader pubertal reorganisation in which the brain is realigned to the social and cognitive challenges of mating. Scherf, Behrmann and Dahl (2012) suggest that the apparently sex-linked or directly sex-hormone linked anatomical and functional changes in cortical face processing regions and subcortical bodies (e.g., to the amygdala) during adolescence may demonstrate a period of increasing specialization for adult sexual behavior. They argue that this realignment may result in temporary disruption of social functions and may underlie phenomena such as the developmental dip in face

processing. Indeed, Scherf et al. explicitly suggest that attraction may be subject to the same disruption as other aspects of face processing, and comment on the current paucity of data assessing this possibility. This suggests that, whereas changes in DHEA may activate the initial onset of adult-like facial preferences, cognitive processing factors may subsequently constrain the expression of preferences until puberty is completed.

Attempts to explicitly link pubertal development to changes in mate preferences and facial recognition alike, however, have yielded mixed results. Typically, researchers use standardized self- or parent-report measures of puberty to assign puberty stages to participants and assess whether stage or raw scores on pubertal development predict preferences/performance (e.g., Boothroyd et al., 2014; Saxton et al., 2010). These puberty measures typically utilize the Tanner classification images or verbal descriptions of physical development that align with the Tanner drawings. Although phenotypic cues to puberty are associated with changes in sex hormones, they remain a blunt instrument in assessing those underlying hormones and are subject to report biases from children and parents alike (see e.g., Carskadon, & Acebo, 1993, for discussion). It is therefore not entirely surprising that Boothroyd et al. (2014) found no link at all between mate preferences and puberty stage, whereas Saxton et al. (2010) found that more advanced puberty was associated with stronger preferences for symmetry, but not for averageness or voice pitch, and that pubertal development had inverse effects on femininity preferences at 12 versus 13-14 years. Kościński found little evidence for breast development as a marker of puberty being linked to girls' preferences for skin health (Kościński, 2011, 2013) and indeed limited evidence for it predicting any other aspects of girls' preferences (e.g., for 'sexy looking' or 'friendly' faces). Only Kościński's (2010) data on 11- and 12-year-old boys showed a strong link between current development and maturity of preferences.

To our knowledge, no researchers have assessed pubertal hormones directly when seeking to test links to mate choice. In a pilot study, Boothroyd and colleagues investigated whether salivary DHEA-S levels (a diurnally stable metabolite of DHEA) were associated with face preferences in a group of 10-year-old children. The resulting data were largely nonsignificant; however in part this may be due to 10 years of age being an inappropriate window for assessing these impacts (Boothroyd et al., in prep). The combined weight of Boothroyd et al.'s (2014) cross-sectional data and Scherf et al.'s (2012) review, regarding activatory and inhibitory periods of change in mate preferences, would suggest that any activational effects of DHEA may best be observed in the 6 to 9 years window, whereas any inhibitory impact of gonadal hormones may best be observed in the 11 to 14 year window. Future research seeking to test the hypothesis that adrenal and gonadal hormones may alternatively activate mate preferences and then inhibit face and other social processing must also concurrently test both mate preferences and facial processing alongside hormone assays in order to fully explore the interactions between the three.

An additional qualification to the mixed results on puberty, however, is that cross-sectional samples may not offer the best determinants of this question. Individual differences in age of puberty are associated with preferences for both faces and voices. Women who experienced first menses at an earlier age prefer more masculinized faces (Cornwell et al., 2006) and deeper voices (Jones et al., 2010) in adulthood. When shown naturally varying male facial stimuli, Hoier's (2003) participants showed a tendency for earlier first menses to predict rating all faces as more attractive than women with later first menses. These differences may reflect the impacts of early stressors on pubertal development (see Deer, Bernard, & Hostinar, this volume, for further discussion) and mate preferences alike or alternatively reflect differences in sexual and romantic experience, arising from earlier vs later menarche, shaping future preferences. For instance, earlier first menses is associated with earlier first coitus (e.g., Downing & Bellis, 2009; Udry 1979) and given the sex difference in age of puberty those early relationships are likely to be with older males. Related to this, Kościński (2010) found that boys' sexual experience predicted similar patterns of face preferences as their pubertal development, highlighting the impact experience may have.

One key problem with the data on pubertal development and mate choice during puberty may thus be that pubertal hormones may have differing effects within and between individuals. Indeed, although breast development was a weak predictor of preferences among Kościński's (2013) female participants within 12- and 13-year-old cohorts, girls with earlier menarche had more adult-like preferences for health, facial 'sexiness,' and facial cues considered by adults as indicating a good partner. Although Kościński viewed time since menarche as an index of relative pubertal development, the fact that breast development showed no strong patterns suggests these data were picking up on timing of previous developments rather than current hormonal status, per se. As such, research into hormonal drivers of pubertal development in mate choice must include longitudinal,

within-individual analyses. Indeed many of the studies that have found hormonal influences on mate preferences in adults have relied on within-individual comparison. For instance, Welling et al. (2008) found no difference between men with overall higher and lower testosterone in terms of their preferences for female femininity; there was, however, a significant difference in mate preferences when comparing between the two sessions in which each man had higher versus lower levels of testosterone.

BOX 1: Facial preferences and parental features

Despite any potential role of innate representations in early preference as per Slater et al.'s (1998, 2000) neonates, later infant preferences are undoubtedly influenced by experience with the faces of conspecifics. For instance, while most studies show a preference amongst infants for female faces over male faces (see, e.g., Ramsey-Rennels et al., 2006, for a discussion), infants whose primary carer is male show a preference for male faces over female faces (Quinn et al., 2002). This strongly suggests that in early life, at least, the primary carer is *the* major influence on facial prototyping and facial preferences (although see, e.g., Cooper, Geldart, Mondloch & Maurer, 2006, for evidence on the potential importance of peers in childhood preferences).

Parental features are also important in attraction in adulthood. The phenomenon of sexual imprinting (whereby an organism bases its choice of adult sexual partner on the features of its parents) is well documented in some animal species (e.g., Zebra finches: Vos, 1995) and has been shown to operate amongst humans, with adults showing preferences for parental features in terms of race (Jedlicka, 1980), coloring (Little et al., 2003), hairiness (Rantala, Pölkki, & Rantala, 2010), age (Perrett et al., 2002), and even personality (Gyuris, Jarai, & Bereczkei, 2010). The ontogeny of this phenomenon, however, remains obscure.

It may be that our facial prototypes are based on the faces we are exposed to, and that although this process is continuous throughout life (e.g., Anzures et al., 2009; Rhodes et al., 2003; Webster & MacLeod, 2011), extensive exposure to our parents in early life heavily biases our prototypes, and ergo our preferences, towards parental features. However, evidence suggests that a degree of associative learning may also take place, with positive parent-child relationships predicting greater imprinting. For instance, Bereczkei and colleagues (Bereczkei, Gyuris, Kovács & Bernath, 2002; Bereczkei, Gyuris, & Weisfeld, 2004) used a photograph-matching task to show that similarity between an individuals' opposite-sex parent and their spouse was significantly greater if the individual reported a warmer relationship with their parent (although see Marcinkowska & Rantala, 2012). Furthermore, Bereczkei et al. (2004) controlled for self-similarity effects and used adoptive fathers and daughters so that genetic explanations can be ruled out. Wiszewska, Pawlowski, and Boothroyd (2007) found that the objective facial proportions of women's fathers significantly correlated with the proportions of faces they found most attractive out of an array, although only if the daughters reported a positive relationship with their father. Similarly, Kocsor, Saxton, Láng and Bereczkei (2016) found that participants who reported less rejecting opposite sex parents had stronger preferences for faces manipulated to resemble that parent.

Developmental research into imprinting-like phenomena is particularly rare. Two studies have demonstrated that children may show a preference for parental features prior to puberty. Kocsor, Gyuris and Bereczkei (2013) used a story-completion task with 3- to 6-year-olds and found that boys who completed a story about a young bird in a storm with the bird flying to one of its parents, preferred father-like faces more than boys who completed the story with a different ending. There was no such pattern for maternal features or in girls. Using more standardized measures of attachment, Vukovic, Boothroyd, Meins and Burt (2015) looked at preference for parent-like faces in 9-year-olds drawn from a longitudinal cohort, and found that although infant attachment as measured in the strange situation paradigm at 15 months did not predict preferences for parental features in either sex of face, children who reported a currently more accepting relationship with their parents (on the Parental Acceptance and Rejection Questionnaire: Rohner, & Khaleque, 2005) favored more parent-like faces. This pattern held for girls looking at both sexes of face, and for boys looking at female faces. For boys looking at male faces, visual exposure predicted preference for paternal features but current relationship did not.

Interestingly, although Vukovic et al. interpreted their data as indicating that parental imprinting may reflect a transient associative impact of positive parent-child relationships on attitudes to parental features, with current experience superseding past experience, Saxton (2016) found that

retrospective reports of parent-child relationships had different impacts in different time periods. Specifically, the similarity of women's ideal/actual partner eye color and their father's eye color was positively predicted by closeness to father in mid-childhood, and negatively predicted by closeness to father after puberty. This would suggest that puberty may act as a watershed for typical imprinting affects and that incest-avoidance mechanisms may come more to the fore once individuals are reproductively mature (although incest-avoidance mechanisms regarding siblings typically have a much earlier critical window; reviewed in Rantala & Marcinkowska, 2011).

Facial preferences and menopause

Further evidence that hormonal changes across the lifespan are associated with variation in mate preferences comes from studies that tested pre- and post-menopausal women. As women approach menopause, estrogens, progesterone, and testosterone decrease and fertility declines (Burger et al., 2002, 2008). Just as preferences for overall attractiveness become more consistent within groups as children age (Saxton et al., 2009), so they may become less so across menopause. Kościński (2011) asked peri- and post-menopausal Polish women aged 40 to 62 years to judge the attractiveness of stimuli of male facial photographs. The post-menopausal women showed significantly greater variation in their preferences and had a lower intra-class correlation than peri-menopausal women of the same age. Studies into specific preferences and menopause have operated on the assumption that the decline in fertility around menopause may trigger a shift away from a mate-oriented mindset toward a community-oriented psychology (Hawkes et al., 1998). Thus, post-menopausal women should be less attracted to indices of mate quality. Furthermore, the decline in sex hormones ought to be associated with a decline in face preferences that are strongly modulated by these hormones.

Considering that previous research has established a small but robust link between women's fertility across the menstrual cycle and heightened preferences for masculinity in particular (Jones et al., 2005a; Little et al. 2008; Welling et al., 2007), research around menopause has also tended to focus on this trait. Vukovic et al. (2009) first investigated the association between fertility across the lifespan and women's masculinity preferences. The authors tested ninety-seven women's masculinity preferences, forty-five of whom were no longer experiencing menstrual cycles due to menopause and all of whom reported that they were not using any hormone replacement therapies or hormonal contraceptives. Participants gave forced choice preferences for pairs of masculinized and feminized versions of both male and female faces. Post-menopausal women had weaker masculinity preferences than pre-menopausal women, but the difference between the pre- and post-menopausal groups was not significant.

One possible reason for this null result may have been the small sample. Little et al. (2010) investigated pre- and post-menopausal women's preferences for facial masculinity in two samples with nearly 200 and nearly 2000 participants, respectively. In Study 1, participants between the ages of 40 and 65 years judged the attractiveness of 10 trials containing masculinized and feminized versions of men's faces. In Study 2, women aged 36-45 years were compared to women over 45 years (amongst other groups). In both cases, post-menopausal participants and/or those aged over 45 years preferred less masculine men than did pre-menopausal/younger women. These results suggest that post-menopausal women are more attracted to the direct pro-social benefits signalled by relatively feminine men (see also Fink & Penton-Voak, 2002; Gangestad & Simpson, 2000; Jones et al., 2008; Little et al., 2002; Rhodes et al., 2005).

Another factor contributing to the weak results in Vukovic et al. (2009) may be that the stimuli used in the study were of young adults. Therefore, it is possible that circum-menopausal women did not view the young male faces used in the study as faces of potential mates. Accordingly, Jones et al. (2011) replicated the study using face stimuli of individuals closer to the age of a new sample of circum-menopausal participants. Results yielded a significant difference between pre- and post-menopausal women's preferences for men's faces, whereby post-menopausal women preferred the feminized versions of the men's faces. Collectively, these results provide evidence for hormonally driven variation in women's masculinity preferences and highlight the importance of testing face preferences using a wide range of stimuli.

It is also worth noting that although Vukovic et al. (2009) and Jones et al. (2011) found an overall preference for femininity, Little et al.'s (2010) participants showed a general preference for masculine men's faces. These results are not surprising considering that other studies have found no consensus as to whether women overall prefer masculine or feminine male faces (see Scott et al., 2014; Fink & Penton-Voak, 2002). It is therefore important for further studies to recruit participants of

various backgrounds, ages, and from different cultures. Also, although masculine men are perceived to look older (Boothroyd et al., 2005; Little et al., 2011) and older women have been found to prefer older faces (Kościński, 2011), the studies on circum-menopausal women's masculinity preferences emphasize that masculinity and perceived age are separate, compound facial traits. As such, manipulations of these independently may differentially influence women's preferences. Moreover, both Vukovic et al. (2009) and Jones et al. (2011) considered both male and female faces. Post-menopausal (i.e., infertile) women preferred more feminine female faces than did pre-menopausal (i.e., fertile) women. The authors controlled for age, suggesting that these results were due to the differences in hormonal profiles between pre- and post-menopausal women. In line with theories of heightened intrasexual competition during periods of high fertility (see Fisher 2004; Jones et al. 2005a; Welling et al. 2007), this research implies that same-sex competition for potential mates decreases as women's fertility declines, and that women may become more honest about the attractiveness of other women as they age (i.e., may be less likely to derogate their competitors).

Another testosterone-dependent masculine trait in men's faces, other than male-typical face shape, and which has been studied in relation to menopause is facial hair. To test out women's preferences for facial hair, Dixson et al. (2012) collected stimuli of men at various stages of beard growth: clean shaven, light stubble, heavy stubble, and full beard. Participants were women in New Zealand of various reproductive statuses who were asked to choose the most attractive of the stimuli presented. Interestingly, post-menopausal women found all the stimuli more attractive than did pre-menopausal women, although cohort effects are possible, suggesting a general shift in baseline thresholds for attractiveness in (young) faces. There was no interaction between menopause and preferences for degree of facial hair in the stimuli, indicating no specific change in attitudes to beards in these groups. Much like in Vukovic et al. (2009), the authors suggested that images of older men should be used in future studies and may yield different results. It is also worth noting that Dixson et al. (2012) found minimal evidence for differences in fertility status in younger women affecting attitudes to beardedness in the same study. As discussed by Dixson et al. (2012), male mate quality is signaled partly by shape-based traits like chins and jaw lines, which are masked by facial hair. As such, beardedness may not show a straightforward relationship with typical predictors of mate preferences, being both a display and a mask of mate quality. Indeed Dixson et al. (2016) showed evidence for an interaction between masculinity and beardedness; extremely feminine and masculine men looked more attractive when bearded, but not men in between. Given the evidence women typically prefer men closer to 'average' levels of masculinity (e.g., Scott et al., 2010), this suggests beards may operate more as a mask than as a signal.

Finally, Kościński (2011) also assessed circum-menopausal women's preferences for mate-relevant aspects of facial appearance, such as health. As in the above studies, preferences for facial health declined with menopause, as did preferences for faces rated by other women as 'sexy' or 'marriageable,' although preferences for 'friendliness' remained constant. Although health preferences are a reasonably objective feature, it should be noted that 'sexiness' and 'marriageability' are inherently subjective constructs shaped in part by the preferences of the perceiver and as such these declines may simply reflect changing definitions of what constitutes sexiness, for instance, in older women. The results are, however, consistent with those presented above for objectively manipulated masculinity and contribute to the overall suggestion that menopause does indeed lead to a decline in those mate preferences commonly ascribed to hormonal factors.

Collectively, the above research suggests that women's preferences for cues of mate quality in men change across the lifespan. Specifically, these studies show hormonally-driven variation in women's attraction to masculinity, health, and sexiness, whereby post-menopausal women tend to prefer more feminine, less healthy, and less sexy (as rated by younger women) individuals than do fertile women. More research is needed, however, to better understand the link between fertility and mate preferences, and how these preferences influence social interactions within this age cohort. For instance, menopause may not proceed in the same manner for all women (indeed, any study relying on proxies of hormones such as cycle phase is subject to this caveat) and, as in the pubertal period, there is a dearth of direct assessments of hormones in menopausal women. As such, suggestions that these changes are directly the result of circulating hormones rather than, for instance, by-products of changing self-rated attractiveness with age, or explicit knowledge of changing fertility and thus changing attitudes toward relationships, remain untested. These findings point to a need for more studies using diverse participants, larger sample sizes, and more diverse stimuli of faces of various phenotypes. Additionally, future studies should employ more hormonal assay techniques to more accurately assess participants' hormonal profiles.

Finally, there is also a need to consider age-related hormonal changes in men, and the impacts of these changes on preferences. To our knowledge, only one study has examined trajectories in heterosexual male preferences for females in later life. Marcinkowska, Dixson, Kozlov, and Rantala (2015) found a fairly linear decline in men's preferences for facial femininity in women between 30 and 70 years of age (although even the oldest participants still preferred feminized stimuli more than chance). This is a period in which testosterone may decline initially through lifestyle factors (e.g., marriage and fatherhood; for review see Gray & Campbell, 2009) and later through aging processes (Harman, Metter, Tobin, Pearson & Blackman, 2001), and thus may lead to decreased interest in indices of female mate quality. However, again, the study was unable to directly assess hormone levels and utilized young female stimuli. Given that feminine faces look younger, it is possible that this decline in part merely reflects an interest in more age-appropriate partners.

Conclusions

There are several key themes that arise when considering these lifespan approaches to mate preferences. Firstly, although there are some aspects of faces about which individuals of all ages from birth through menopause consider attractive, preferences for specific aspects of faces, voices, and bodies that have been linked to mate quality in adults are subject to change over time. When we consider patterns across mid-childhood and menopause, it seems likely that pubertal hormones may activate specific mate preferences, whereas menopause and the corresponding decline in sex hormones may lead to a decline in mating-relevant preferences. Similarly, although there is apparent disruption of preference development mid-puberty, this too is plausibly the result of sex hormones changing social perception in general in line with the further activation of mating-relevant cognition.

There remain, however, some key weaknesses in this literature. Firstly, a complete dearth of direct assays of circulating hormones in the participant groups in question means that it is difficult to strongly conclude that hormonal factors are indeed driving these changes. Furthermore, studies rarely – if ever – consider other potential mediators, such as broader face processing during childhood and puberty, or mating versus social attitudes in menopause, in the same samples. Although these mediators may work in tandem with the impacts of sex hormones, rather than as alternative explanations, not assessing them alongside mate preferences limits our understanding of the processes driving change across these periods. This weakness is particularly pertinent when considering the infant literature; although circulating sex hormones are high in early infancy, limitations in face processing likely have a strong impact on expressed face preferences. Thus, although there may be a fruitful narrative to be developed in the future regarding, for instance, organizing effects of hormones *in utero* and infancy, or even the possibility that sex hormones may direct attention to mate-relevant traits even in this early period, without both measuring hormones and controlling for broader face processing, it will be impossible to further consider these possibilities.

Likewise, the lack of within-participant comparisons in much of the literature is a serious weakness that urgently needs to be addressed in order to disentangle within- and between-individual differences in hormones and the differing sources and potential impacts on preferences these may have. Furthermore, the wide degree of variation across studies in terms of the age of the stimuli used, the precise manipulations used, whether or not stimuli were masked, and the way hormonal proxies are assessed (e.g., puberty scales, breast development, reported menstruation, age) also clouds our ability to confidently interpret the overall results for any given trait of interest. The result of these caveats, however, is that we perceive here a literature that is ripe for further research, which may yet yield a truly comprehensive and coherent model of how sex hormones impact on the development and expression of mate preferences across the lifespan.

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