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Article

Beautiful fruits taste good: the aesthetic influences of fruit preferences in humans

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With 3 figures and 1 appendix

Summary: Although diversity of fruit/seed colouration has received a great amount of attention since Darwin, little is known about its role in eating preferences in humans. We have determined that humans prefer certain fruits/seeds over others and that their willingness to eat them has been significantly influenced by the perceived aesthetic of the presented fruits and seeds. Participants were unable to discriminate between edible and poisonous fruits/seeds based on their colour. Females rated all the groups of fruits/seeds as more attractive than males with this supporting the role of females in picking fruit in our evolutionary past. Red fruits were rated as more attractive than green or brown fruits. The results support the idea that fruit/seed colouration plays an important role in plant – disperser coevolution and that aesthetic judgment in humans have been shaped by natural selection.

Key words: evolution, colour, diet, fruit, human, preference.

Introduction

The fruits of various plants show amazing diversity in both colours and sizes. Despite scientists having shown a serious interest in this topic since Darwin (1874), the evolutionary pressures responsible for fruit colour diversity are still not fully understood (Willson & Whelan 1990). It is assumed that the limited dispersal abilities of plants are balanced by their investment into fruit colouration. Fruit conspicuousness is viewed as an adaptation in order to increase the detectability of plants for potential seed dispersers for nutritious rewards (Ridley 1930, Schmidt et al. 2004). This mechanism would be plausible in particular with diurnal, colour-sensitive animals (Wilson & Comet 1993) such as frugivorous birds showing preferences for certain fruit colours relative to others (Willson 1994, Willson et al. 1994, Puckey et al. 1996, Siitari et al. 1999, Burns & Dalen 2002, Whitney 2005, Schaefer et al. 2008).

Most mammals have dichromatic vision, although a number of primates are an exception (Jacobs 1993). Among anthropoid primates, a trichromatic vision in both sexes is known in Old World monkeys, apes and humans (Jacobs & Deegan 1999, Regan 2001, Domini et al. 2003). Trichromatic vision is determined by the presence of three distinct types of retinal cone photoreceptors. These different types contain short-wave (S) sensitive cones with a pigment reaching peak sensitivity between 420

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and 430 nm, and middle-wave (M) and long-wave (L) sensitive cones with pigments reaching peak sensitivities between 530 and 565 nm. Trichromacy is superior to dichromacy and may indeed be optimal for finding or recognizing edible fruits and leaves (Osorio & Vorobyev 1996, Regan et al. 2001, Osorio et al. 2004).

Most primates are arboreal with their food consisting in particular of leaves, fruits, and flowers of tropical forest trees (Wrangham 1998, Milton 1999, Ungar & Teaford 2002). Modern humans evolved from a chimpanzee-like ancestor (Pilbeam 1996). The anatomy and physiology of the digestive system (Milton 1986, Milton & Demment 1988), microbial communities within the primate gut (Ochman et al. 2010), and neural activity in the taste perception (Scott 2010) of humans and recent anthropoids is similar, suggesting certain similarities in diet preferences between human ancestors and other primates (Milton 1999, Ungar & Teaford 2002, Babbitt et al. in press). The diet of contemporary humans is particularly influenced by the adoption of agriculture which is dated at only some twelve thousand years ago (Ungar & Teaford 2002). The ancestral line leading to extant chimpanzees and modern humans, however, may have diverged as recently as 4.5 mya (Takahata et al. 1997). This would mean that for the majority of human existence members of our genus (*Homo*) have lived as hunter-gatherers (Laughlin 1968, Conroy 1997).

The forager diet reconstructed by Eaton et al. (1985, 1997) contained 35 % meat and 65 % wild plant foods. Trichromatic vision in hunter-gatherers favoured the detection of fruits, seeds or other sources of food. The role of the gatherer was typical for females, while males were predominantly hunters (Kaplan 1996). There are, however, certain documented exceptions to this general pattern. A study carried out with the Aeta people of the Philipines, for example, determined that approximately 85 % of Philippine Aeta women hunt and have greater success hunting rates than men (Dahlberg 1975). Kuhn & Stiner (2006) have proposed that the sexual division of labor did not exist prior to the upper Paleolithic period, which lasted from about 45,000 years ago to 10,000 years ago, but developed relatively recently in human history. The sexual division of labor may have arisen in order to allow humans to acquire food and other resources more efficiently.

However, not all coloured fruits are edible; instead strong and contrasting colours (red, yellow, black or brown) often characterize aposematic unpalatable or poisonous species (Edmunds 1974, Gittleman & Harvey 1980, Lev-Yadun 2001). How then did our ancestors discriminate between edible and poisonous sources of plant food? Recent non-human primates have a preference for certain colours (especially reddish or yellowish fruits associated with ripening) over others (Urbani 2002, Caine et al. 2003, Smith et al. 2003, Melin et al. 2009). Humans prefer red over the green colour (Maier et al. 2009) with this preference for red being more pronounced in females (Hurlbert & Ling 2007), in all probability assisting them in finding ripe fruits and berries on a background of green leaves (Heerwagen & Orians 1993, Hurlbert & Ling 2007). This is also supported by the higher preference for berries by Hadza females who are hunter-gatherers in Tanzania (Colette & Marlowe 2009). In addition, Mexican females are able to collect more mushroom species and find more collection sites at a lower energy cost than Mexican males thereby supporting the idea that females, but not males, excel at tasks appropriate to the gathering of immobile plant resources (Pacheco-Cobos et al. 2010).

Although data on fruit preferences in humans are scarce, evolutionary research indicates that the aesthetic judgment of humans has probably played an important role in everyday decisions (Voland & Grammer 2003). From early life, humans have attributed positive qualities to attractive subjects and negative qualities to unattractive subjects, a mechanism known as "what is beautiful is good" (e.g., Dion et al. 1972, Dion, 1973, Langlois et al. 2000). Evolutionary biologists implicitly suggest that the mechanisms responsible for preferences of beauty have evolved under sexual selection. That is, the preferences of a physically attractive partner are ultimately preferences of "good genes" (Langlois 2000), which has recently been supported by molecular analyses (Lie et al. 2008). Studies concerning the influence of natural selection on beauty preferences are still scarce, however.

This study examined whether the evolved perception of beauty in contemporary humans would influence the preferences of various fruits or seeds, sources of food which have heavily influenced the fitness of our ancestors. Perception of pigments which impart colour in ripe fruits and vegetables, such as chlorophyll, carotenoids and anthocyanins (Lancaster et al. 1997) would provide useful information to a receiver and activate his or her aesthetic judgment. Moreover, sensory factors such as colour or shape are more important for human food preferences than the metabolic equivalence in terms of protein, carbohydrates and fat content (Rolls 1997). We predict that fruits or seeds that will be perceived as more attractive would be considered more edible than less attractive fruits. In addition, we predict that females would be more sensitive to the aesthetic value of fruits or seeds as a result of their role as gatherers in our evolutionary past.

Methods

The sample

The sample of participants (106 males and 89 females) consisted of 10–15-year-olds attending two randomly selected primary schools in Western Slovakia. The mean age of the participants was 12.3 years (SE = 0.09). The participants were asked (a) for their age/grade and (b) for their sex.

Measuring of aesthetics, edibility, and willingness to eat fruits

We presented 20 colour pictures of unfamiliar fruits in lecture halls (see Appendix). We adjusted the picture sizes to a standard body length. The pictures had a similar contrast and brightness. The pictures were presented in a random order. Each picture was presented for 1 min. During this time, the participants rated the aesthetics of the fruits (To what degree do you consider this fruit attractive?), willingness to eat the fruit (To what degree would you would like to eat this fruit?) and edibility (To what degree do you consider this fruit poisonous?) each on a 5-point scale (e.g., 1 = not at all, 5 = extremely beautiful). All the dimensions revealed acceptable reliabilities (Cronbach alpha = 0.78, 0.76 and 0.55, respectively). In addition, the participants were asked about their experience with each fruit (Have you ever seen this fruit?) and about their identification skills (Do you know the name of this species?). None of the participants reported having had experience with the fruits or any of the names of the presented species. Thus, we conclude that the children were not familiar with the presented fruits and that these two variables were not involved in further statistical tests.

Categorizing of the aesthetics of fruits

We performed an additional study in which we asked a separate sample of 10–11 year old primary school children (n = 21) and a sample of university students aged 22–24 (n = 15) to rate the aesthetics of 20 fruits prior to the final study. The participants were unaware of the edibility or species identity of the fruits. The mean scores of both school children and university students strongly correlated with the means of a focal sample (n = 195) (r = 0.79 and 0.86, both $p < 0.001$, respectively). These results provided further support as to the reliability of the ratings of attractiveness. We categorized 11 fruits with high mean scores (M = 3.64, SE = 0.08) and 9 fruits with low scores (M = 2.84, SE = 0.09) as "attractive" and "unattractive", respectively. Differences in the mean ratings of attractiveness between the two groups were significant (t-test, t = 6.21, df = 18, $p < 0.001$). For statistical analyses, we divided fruits into 4 groups: attractive and edible (n = 6 species), attractive and poisonous (n = 5 species), unattractive and edible (n = 4 species) and unattractive and poisonous (n = 5 species).

Results

Relationships between perceived aesthetics, poisonousness and the willingness to eat fruits

A series of Pearson correlations revealed that the perceived aesthetics positively correlated with a willingness to eat edible and poisonous attractive and unattractive fruits (r = 0.37, 0.39, 0.29 and 0.35, respectively, all $p < 0.001$, n = 195, Fig. 1). The perceived aesthetic negatively correlated with the perceived poisonousness of the edible and toxic attractive and unattractive fruits (r = –0.26, –0.15, –0.26 and –0.07, respectively, all *p*'s except for the last correlation were significant at 0.05 and less, n = 195). The perceived poisonousness negatively correlated with the willingness to eat both poisonous and edible attractive and unattractive fruits (r = –0.50, –0.31, –0.47, –0.25, respectively, all $p < 0.001$, n = 195).

Gender differences in perceived aesthetics, poisonousness and willingness to eat fruits

A series of t-tests revealed that females rated the aesthetics of all kinds of fruits higher than males (Fig. 2). There were no differences, however, in the willingness to eat poisonous fruits or in the perceived poisonousness between males and females (t-tests, all *p*'s > 0.15).

Effects of edibility and perceived aesthetics on children's willingness to eat fruits and perceived poisonousness

The multivariate analysis of variance (MANOVA) with edibility (edible vs. poisonous) and the perceived aesthetics (attractive vs. unattractive) as independent variables and the mean scores of willingness to eat fruits and perceived poisonousness as dependent variables revealed that both aesthetics and edibility influenced the dependent variables (Wilk's lambda = 0.98 and 0.97, $F(2,775) = 7.69$ and 8.56, both $p < 0.001$, respectively). The interaction term was also significant (Wilk's lambda = 0.98, $F(2,775) = 7.16$, $p < 0.001$). The inclusion of the effect of gender did not influence these results. Attractive fruits were considered more edible than unattractive fruits and poisonous fruits were considered less edible than edible fruits ($F(1,773) = 15.40$ and 12.71, both $p < 0.001$, respectively). Attractive fruits were less likely considered poisonous and poisonous fruits were more likely considered poisonous ($F(1,773) = 2.07$ and 10.77, $p = 0.15$ and 0.001, respectively). Children showed the lowest willingness to eat poisonous and unattractive fruits (Fig. 3). In contrast, toxic and unattractive fruits were perceived as the most poisonous (Fig. 3).

What makes fruits attractive?

After categorizing the fruits into three colour groups (red/orange, green, brown/yellow), the effect of edibility on rating attractiveness was not present, however, red fruits were rated as more attractive than others (a logistic regression with the aesthetic of fruit [attractive vs. unattractive] as a dependent variable, Wald's $\chi^2 = 1.38$ and 4.85, $df = 1$, $p = 0.24$ and 0.03, respectively). All 9 red fruits were viewed as attractive, while in contrast, 5 of 6 green fruits (as well as 4 of 5 brown/yellow fruits) were unattractive.

Discussion

This study reveals that the perceived aesthetics significantly influence the preferences for certain species of fruits and seeds in contemporary humans. In addition, the aesthetic judgment of females was stronger than that of males. Finally, although we were not primarily concerned with colour preferences themselves, this study indicates that red fruits are more attractive than green and brown fruits.

The participants showed a non-random preference for certain fleshy fruits and seeds (in particular those that were red coloured) suggesting that plants attract humans in a similar way as other seed dispersers such as birds (e.g., Puckey et al. 1996, Siitari et al. 1999, Burns & Dalen 2002, Schaefer et al. 2008) or non-human primates (Urbani 2002, Caine et al. 2003, Smith et al. 2003, Melin et al. 2009). Leaf eating primates, for example, preferentially eat the red tinted young leaves because they contain more protein and potentially less toxins and fiber (Dominy 2004). The perception of beauty seems to play an important role in the process of fruit selection. Previous research examined the role of aesthetic judgment within the framework of sexual selection leaving the effects of natural selection unexamined. The selection of colourful fruits or seeds could have had a serious impact, however, on the survival of our ancestors, thus it is reasonable to suggest that a preference for beauty could be influenced by natural selection. As far as we know, this is the first study indicating that the "what is beautiful is good" stereotype (e.g., Dion et al. 1972, Dion 1973, Langlois et al. 2000) works within the context of natural selection. Attraction to certain fruits or seeds, of course, does not mean that more attractive fruits are always edible. In contrast, the edibility of the attractive, but poisonous fruits, was rated similarly to the edibility of attractive and edible fruits. Thus, the perceived attractiveness activates the *initial* willingness to eat these fruits and seeds, although additional senses such as olfaction (Hoover 2010) and taste in all probability influenced the *definitive* decision as to whether a chosen fruit or seed would be consumed or not (for a review, see Birch 1999). This is supported by the research of Hiramatsu et al. (2009)

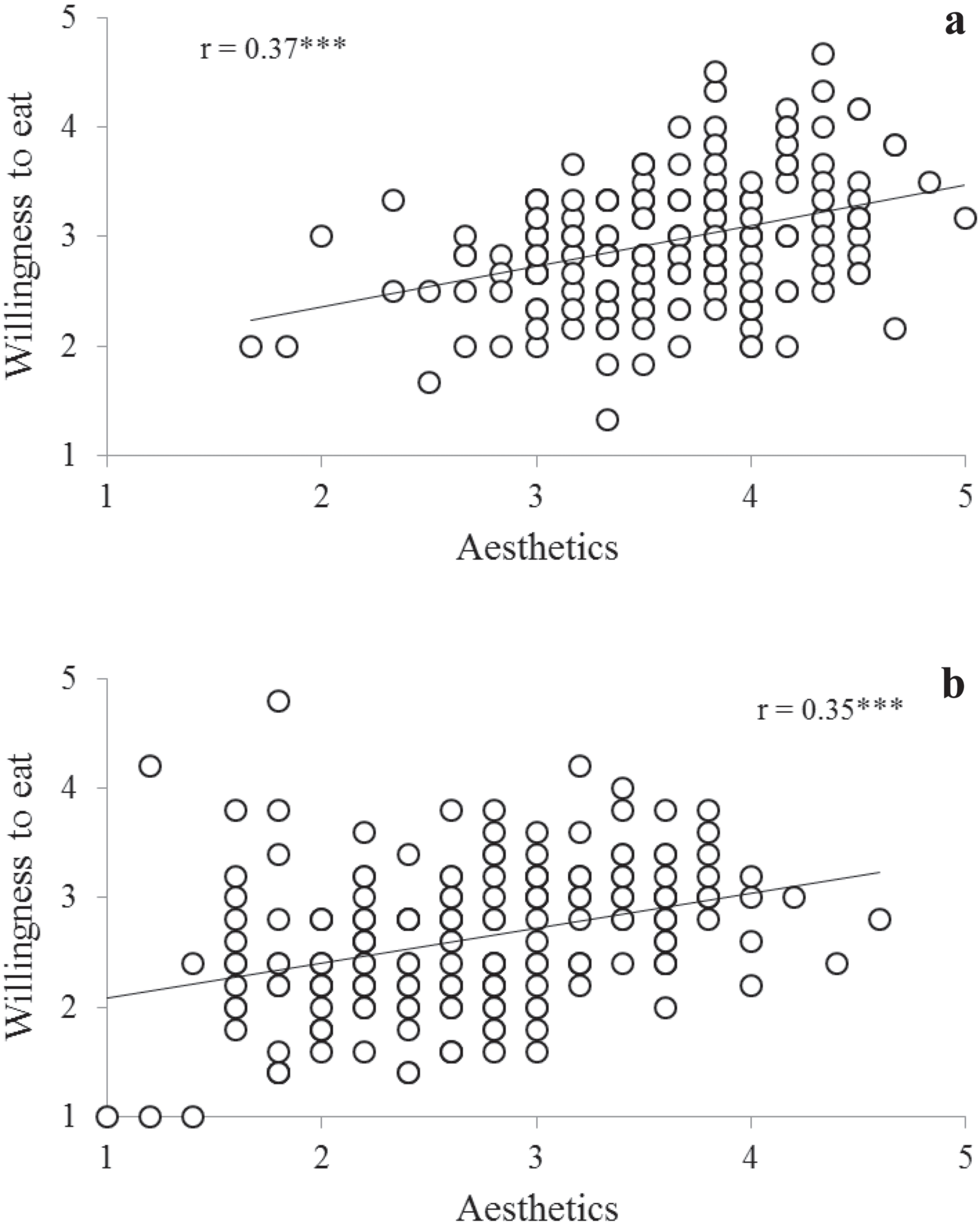
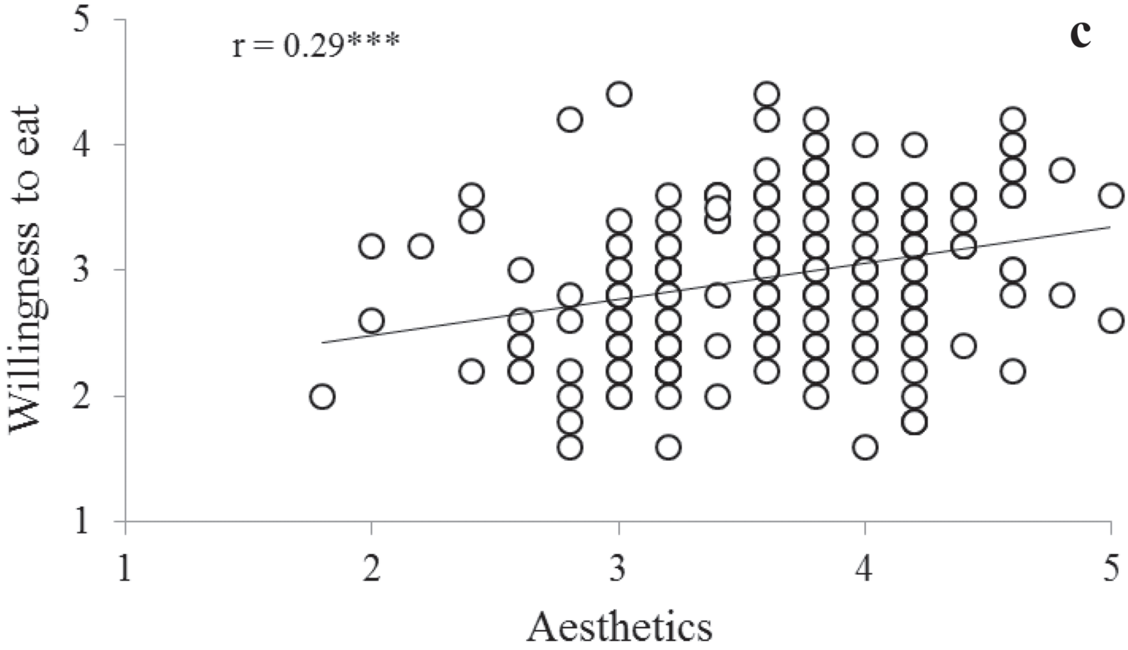


Fig. 1. The relationships between the mean scores of perceived aesthetics and willingness to eat **(a)** attractive and edible fruits, **(b)** unattractive and poisonous fruits, **(c)** attractive and poisonous fruits and **(d)** unattractive and edible fruits.


r = 0.29***
c
Willingness to eat
Aesthetics
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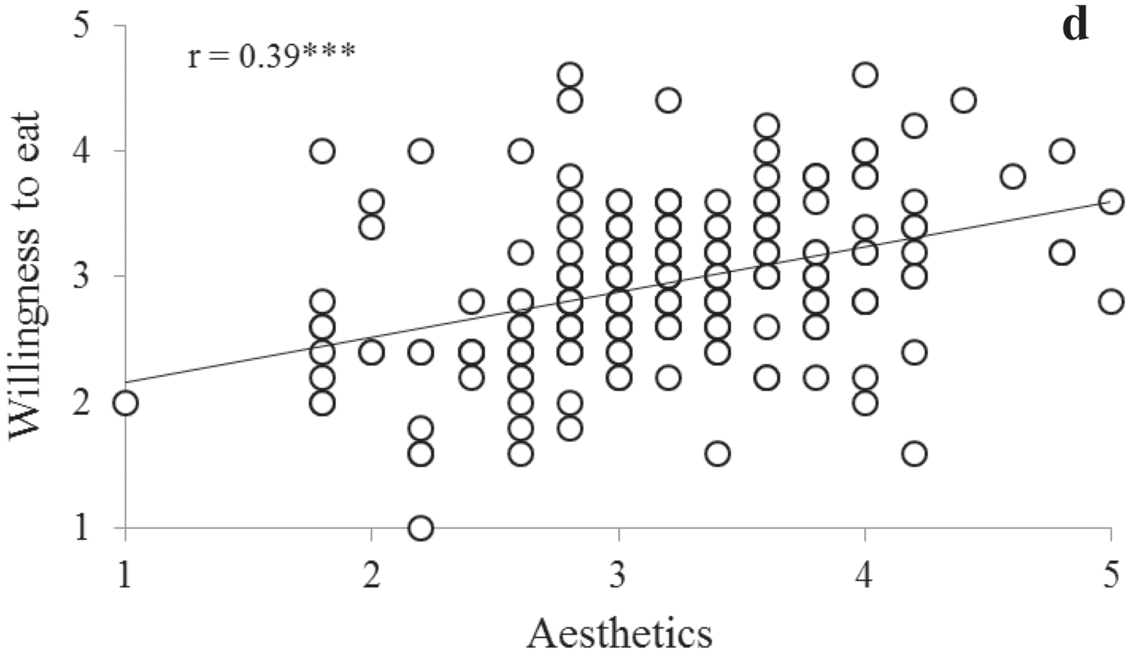
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Aesthetics
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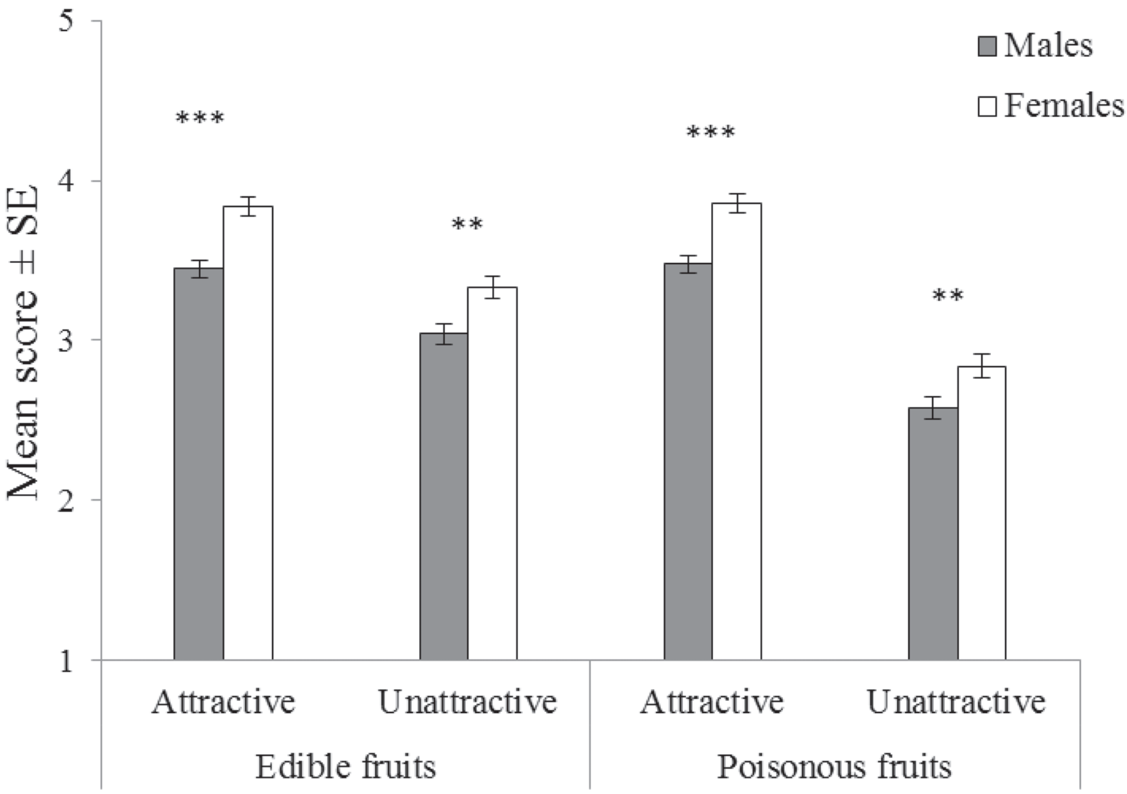

Fig. 2. Gender differences in ratings of aesthetics of four groups of fruits. Asterisks denote significant differences between males (n = 106) and females (n = 89) (***p* < 0. 01, ****p* < 0.001).

who discovered that monkeys use olfaction for discrimination between edible and inedible fruits when vision alone is insufficient to evaluate the quality of the fruits. Furthermore, ancestral humans could copy the foraging behavior of other, more experienced individuals in a social group or even the foraging behavior of other primates. Relatively low negative correlations between unattractiveness and perceived poisonousness and the willingness to eat unattractive fruits could be partly influenced by still unfinished food preferences (Birch 1999). Data obtained from older participants, independent of their parents, could provide more stable and stronger results. At present, it is probable that humans are not able to discriminate between poisonous and edible fruits based on their colour which can be supported by incidents involving children being poisoned by toxic fruits (Litovitz et al. 1992). The edibility of fruits is further complicated by the different types of seed dispersers which have different visual systems and therefore perceive fruits differently (Burns et al. 2009). Moreover, certain fruits of contrasting colours often characterize unpalatable or poisonous species (Edmunds 1974, Gittleman & Harvey 1980, Lev-Yadun, 2001) which further complicates the foraging decisions of seed predators. Alternatively, the influence of an advertisement of unnatural images of fruits is often associated with "healthy products". This could have an impact on perceiving colourful fruits as edible.

In line with our expectations, the aesthetic judgment of females was always stronger when compared with males (Hurlbert & Ling 2007). Females could be attracted by colourful fruits due to the fact that the bright colouring signalled food resources

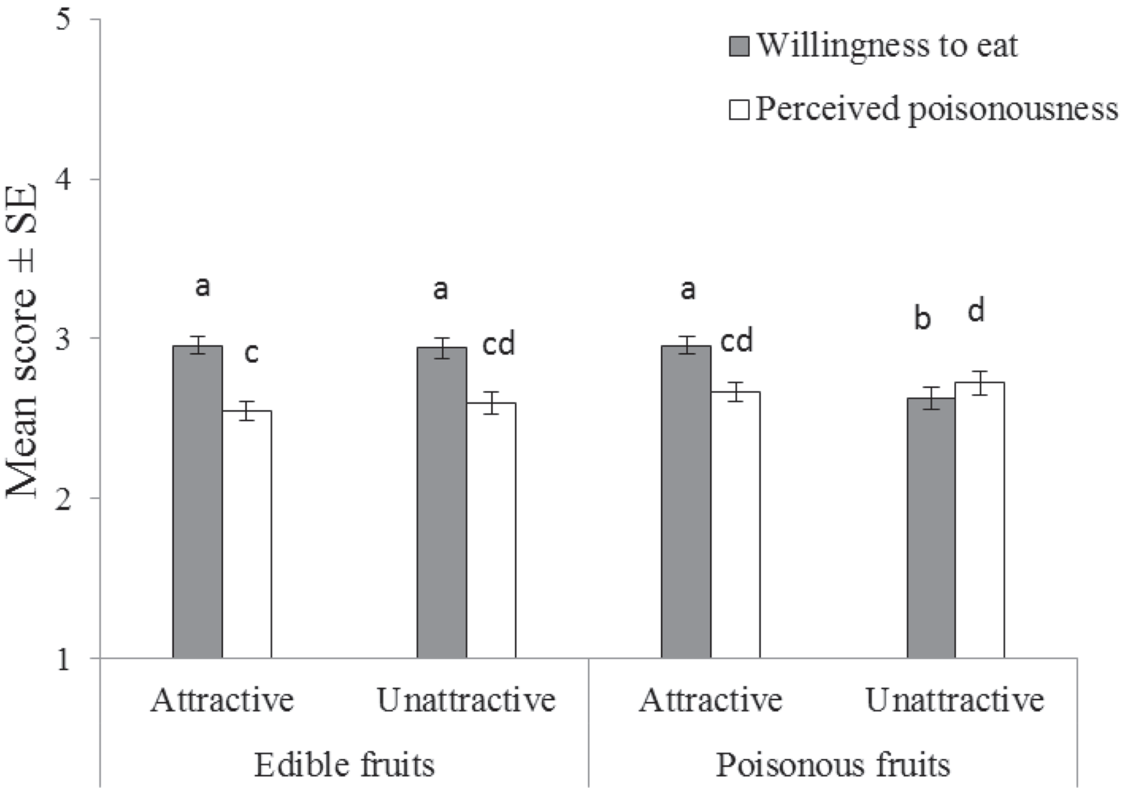

Fig. 3. Differences in children's willingness to eat and perceived poisonousness. Letters above bars denote differences based on pairwise Tukey post-hoc tests. a vs. a (ns), a vs. b ($p < 0.001$); c vs cd and cd vs. d (ns), c vs. d ($p = 0.005$).

for people throughout evolutionary time (e.g., Heerwagen & Orians 1993, Regan et al. 2001). This sensitivity seems to be crucial for survival considering that most of the forager diet consisted of wild plant foods (Eaton et al. 1985, 1997) and females were predominantly gatherers (Kaplan 1996, Colette & Marlowe 2009). At first glance, our results would provide further support for the role of females as gatherers in our evolutionary past. We did not, however, find any gender difference in the ratings of fruit/seed poisonousness or the willingness to eat them. Similarly, certain field studies have failed to determine that trichromatic non-human female primates are more efficient foragers than males (Dominy et al. 2003) or that they prefer red fruits over green cryptic fruits (Dominy 2004). It is therefore difficult to support the assertion that selection has acted differentially in order to enhance female aesthetics in ways that increase the genetic fitness related to the role of gathering/ foraging activities in our evolutionary past. One could argue that females should be more cautious in the selection of foods than males because they invest more in reproduction than males and should provide more care for the offspring. It is therefore also possible that the division of labor whereby men hunt and women gather wild fruits and vegetable is a phenomenon with a surprisingly short evolutionary history (Stange 1997, Kuhn & Stiner 2006). In the future, one might, for example, test whether females caring for their small children would exhibit more conservative behavior in terms of the selecting of certain fruits or seeds more critically than single females. Further research on adult participants, with or without dependant children, is required in order to address this question.

Although our research has not been primarily focused on examining the preferences of fruit and seed colours, red coloured fruits were apparently rated as more attractive than other fruits. This is in agreement with the general preference for the red colour in humans (Maier et al. 2009). It may be that most fruits consumed by our ancestors were red coloured or that an additional property of fruits and seeds (such as shape, odour) could influence red fruit/seed preference. Alternatively, preferences for the red colour could be shaped by sexual selection, in light of the fact, for example, that red ischial callosities in female baboons are cues for sexual receptivity (Fernandez & Morris 2007). In fact, this preexisting bias toward the red colour would explain the increased sexual attractiveness of females dressed in red clothes (Elliot & Niesta 2008). Further archeological, comparative and experimental evidences would be required.

In conclusion, we demonstrated that contemporary humans have a preference for certain fruits and seeds over others and that these preferences are significantly influenced by their attractiveness. The attractiveness of fruits and seeds influences initial foraging decisions such as the willingness to eat these fruits or seeds and the perceived poisonousness of these food sources. Females revealed a stronger aesthetic judgment in terms of fruits and seeds than males suggesting that their role as gatherers in our evolutionary past would still play a role in colour preferences in humans. These results are restricted, however, to 10–15-year-old children who are still maturing, and it is not clear if the adult population (males and females) would make judgements regarding fruits/seeds and their toxicity in the same manner. Teenagers usually have a lower self-preservation level, less experience in food preparation and selection in comparison with the adult population. We hope that our results will encourage other researchers to investigate the role of fruit/seed colouration, shape, size, olfaction, poisonousness, nutrition value or accessibility in the feeding preferences of contemporary humans of various age groups. This will assist us with a deeper understanding of plant – disperser coevolution and with the foraging behavior of our ancestors.

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Appendix. List of plant species used in PowerPoint presentation.

Species	Common name	Fruit (*f*) /seed (*s*)colour
Cornus mas	Cornelian cherry	red[f]
Conium maculatum	Poison Hemlock	green[s]
Euonymus europaeus	European spindle	pink[s]
Morus rubra	Red Mulberry	purple[f]
Passiflora mollissima	Banana Passion Fruit	green[f]
Laburnum anagyroides	Common Laburnum	brown[s]
Diospyros kaki	Kaki Persimmon	orange[f]
Solanum pseudocapsicum	Jerusalem cherry	red[f]
Durio zibethinus	Durian	green[s]
Ilex verticillata	American Winterberry	red[f]
Lantana camara	West Indian Lantana	green[s]
Schizandra chinensis	Schisandra chinensis	red[f]
Tamarindus indica	Tamarind	brown[s]
Chimonanthus praecox	Japanese allspice	brown[s]
Averrhoa carambola	Carambola	yellow[f]
Phytolacca americana	Common Pokeweed	purple[f]
Psidium guajava	Apple Guava	green[f]
Aucuba japonica	Japanese Aucuba	red[f]
Chrysophyllum cainito	Star apple	brown[f]
Styphnolobium japonicum	Pagoda Tree	green[f]

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