The Evolution of Aesthetics and Beauty

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Abstract and Keywords

For over two millennia philosophical discussions tied aesthetics mainly to art and led to meager insights, if any, into why humans experience aesthetic reactions. Current scientific discussions on the issue, on the other hand, have turned to biology, evolution, and neuroscience. They link aesthetics with beauty in art, faces, scenery, and a variety of other sources. The biology of beauty is now viewed as having roots that extend far into the human ancestry, specifically to animal mate selection strategies. This chapter traces and explains the biological role in the human beauty response and its usefulness in various domains of human interactions.

Keywords: Evolution and beauty, brain and beauty, mate selection, art, artistic, attraction, music

Introduction

Aesthetics and beauty-related issues were guided mainly by philosophical debates in the past several millennia (Goldblatt, Brown, & Patridge, 2017), and although the discussions were intellectually useful, the essence of aesthetics remained an enigma until relatively recently. Those debates tied the notion of aesthetics mainly to art, but current scientific explorations have profitably blurred the distinctions between art beauty, face beauty, and other sources of beauty, seeking insights, instead, through aesthetic/beauty reactions in the brain (reviewed in Nadal, 2013; Vartanian & Skov, 2014) as well as through biological explanations. The link to biology was introduced by Charles Darwin in the 1800s, and 100 years later elaborated upon substantially by other scientists (described below). In the 1970s, Amotz Zahavi, an evolutionary biologist, significantly advanced the biological link notion by explaining the intersection of mate selection strategies, art, and aesthetics (Zahavi, 1978). His ideas were subsequently richly developed by Geoffrey Miller, who shone additional well-thought-out light on the biological links (Miller, 2000, 2001).

Unlike Darwin, Alfred Wallace, an evolutionary biologist also working in the 1800s, steered away from the aesthetic issue, emphasizing instead that the basis of females' choice in procreation is an assessment of the qualities of health and strength in the male animal. Such factors underlie the choice since they lead to survival of the offspring (Cronin, 1992; Prum, 2012; Wallace, 1870). The logic behind species survival through selection based on high genetic qualities explains the evolutionary development of elaborate mate-attracting strategies upon which females can base their choice for mating, as in overly large physical characteristics (phenotypes). This exaggerated growth in size and color variations has come to be known as the Fisherian runaway principle (Fisher, 1915). In evolutionary perspectives, the advantage of exaggerated phenotypes is that they reveal multiple important health-related details that are predictive of fitness, and thus have a long-term adaptive value for the species, an advantage that outweighs the risks of exaggeration (susceptibility to predators, increased requirement for maintenance energy). The significance of such notions to the present discussion is that they have helped pave the intellectual road toward explaining aesthetics/beauty reactions in biological terms.

Biological Foundation of Aesthetics/Beauty and Art

Zahavi (1978) proposed that the exaggerated phenotypes, although forming a platform for showcasing and assessing genetic qualities, carry a cost, a handicap. Maintaining the appearance of health requires much effort and only the strongest and fittest can sustain it. The two are intertwined—males' phenotypes allow inspection by the females of minute health-revealing fine details and at the same time the healthiest males, who have high-quality genes, possess the exaggerated physical characteristics. He considers them "decorative patterns" and likens them to the efforts humans put into art-making.

Against this pivoting theoretical backdrop, the artistic genetic qualities can be inferred: they are revealed in the artist's artwork. The more effort artists invest in their artwork, the more they exhibit their artistic genes, which encompass artistic cognition, talent, skill, and intellectual energy. The viewer of the artwork is basically assessing the artist's genes as they pertain to art. The aesthetic reactions in the viewer are positive when the artistic gene quality is high but low or neutral when quality is low. Aesthetics in art, then, using biological terms, are viewers' reactions to those artistic genetic qualities.

Relationship of Mate Selection Strategies to Aesthetics/Beauty

In biological terms, the aim of breeding strategies is, ultimately, propagation of the species. The specifics of the displays are unique to each animal, and nature is replete with examples of the cleverness and variability that have evolved to attract a mate (Gould & Gould, 1989). Regardless of the animal and the details revealed in its unique physical exhibit, (1) the intensity and effort invested in advertising the signals form a fundamental aspect of signal generation, and (2) attention-getting is the overarching goal. Both of these aspects orchestrate the biological logic of the display. To be able to interpret the signals (3) multi-modal brain regions are required in the recipient and, by inference, (4) a co-evolution of the brain of the signaler and of attentional mechanisms of the recipient. These notions are developed further below.

The classic example is the courtship display of the peacock, *Pavo cristatus*, for the benefit of attracting a peahen (Cronin, 1992). The long-feathered peacock tail is lifted into a fan that the animal vibrates to display the "eyes" on the feathers as well as the physical strength required to maintain the vibration. Strutting back and forth in front of her allows the peahen to assess details that would otherwise be hidden when the tail (also known as train) is down and dragged behind. The vibration in the air caused by "rattling" of the raised fan-like tail is achieved not only through the biomechanics of feather structure but also by sheer motoric strength (Dakin, McCrossan, Hare, Montgomerie, & Amador Kane, 2016). The display requires the functionality of several modalities in the peahen's brain. She has to be capable of analyzing feather asymmetries, discoloration, and aberrant iridescence; all could be symptoms of parasite hosting (Balenger & Zuk, 2014; Hamilton & Zuk, 1982), disease manifestations, or outcomes of unsuccessful fights. These would indicate poor fitness qualities and not an inheritance the peahen wants to pass on to her offspring, since she alone carries the burden of hatching and caring for them.

Perceptually and cognitively, the brain of the peahen is suited to discern fitness and genetic qualities in the peacock. To the peahen, the purpose of the display is anchored in biologically practical, species-survival issues for that particular biological pheasant family, not at all what the peacock's physical features signify to human viewers. It is thus reasonable to assume that co-evolutionary processes were underway to match the courtship display needs with the brain and age of the animal observer (a topic elaborated upon subsequently). The animal observer possesses the neuroanatomical underpinning for perceptual and cognitive assessment of genetic qualities in her conspecific. Humans have no way of determining whether or not animals have aesthetic reactions.

To humans, on the other hand, the peacock's feathers are aesthetically pleasing—they provide material and ideas for home decoration, body ornaments, artistic design themes, and inspiration for color fads. None of the fitness signals emanating from the peacock is meaningful procreation-wise to the human observer, indeed they largely go unnoticed.

The feathers are elaborate physical "engineering feats" (Dakin et al., 2016; Yoshioka & Kinoshita, 2001; Zi et al., 2003), so much so as to suggest nothing but evolutionary progress in a trajectory that has been underway for hundreds of millions of years, its purpose being to maximize high genetic inheritance of future offspring. There is fossil evidence of colors and iridescence of feathers going back to the days of the dinosaurs (Hu et al., 2018; Zhou, 2014), long before the peacock and the peahen evolved. The patterns are designed for multi-modal perception, not just for visual assessment. Sounds, air vibrations, and biomechanical effects all require multiple processing of physical entities by the peahen. Indeed, peacocks are not alone among avians in producing multiple effects: several birds such as the hummingbird (Clark, Elias, & Prum, 2013), sage-grouse (Koch, Krakauer, & Patricelli, 2015), the manakin (Bostwick & Prum, 2005), among others (Bostwick,Elias, Mason, & Montealegre et al., 2010) have been found to use biomechanical features to attract a mate. These features send nonvocal signals not readily perceived by human sensory organs.

Additional physical phenotypes advertise fitness in male animals (Gould & Gould, 1989). Antlers are signals of maleness in sexual mate selection. They can be elaborate as in the red deer, elk, or in the caribou. Large bony structures protruding from males' heads, such as horns in cattle or in mountain sheep, are similarly used to advertise strength, dominance, and to win the right to procreate with females. Antlers and horns are cumbersome and pose obstacles in escaping predators. However, they, too, have been evolving in structural composition and function for hundreds of millions of years, and as fossil records indicate, were already present at the time of the dinosaurs (Farlow & Dodson, 1975; Hone, Wood, & Knell, 2016).

The time frame in the foregoing suggests that the basis for aesthetic sensibility in female animals, if it exists, has not changed much in millions of years, unlike aesthetic responses in humans where cultural habits and conventions have an impact, and many beauty-related habits have short duration times. The interaction of the biological roots with human fashion fads and ever-changing values enter into humans' aesthetic reactions. Thus, although Darwin was the first to think of biological reasons, significant insights, relevant ideas, and inferences regarding the relationship to art were discussed and gained much later (as reviewed above; and see Jones & Ratterman, 2009).

Darwin, when he suggested that the whole appearance of the peacock (and other male animals) was influenced by female aesthetic sensibility (the peahen's), could not have known that future scientific investigations would reveal, more than 150 years later, minute physical and chemical arrangements in the peacock's feathers, namely that biomechanical aspects of the feathers enter into the courtship display strategy, and any aesthetic "taste" in female animals could not have led to such a complex arrangement in the male. The most parsimonious explanation for so-called female choice strategies is to assume that natural selection "selected" those features that reveal genetic qualities the most even if that means extravagant appendages. In other words, the more is revealed, the more informed the choice. The biological evolution of the male's feathers could have evolved independently of the observer's "taste." It has been argued that male competition alone plays a major role in this process (see Moore & Martin, 2016). Whatever the form the physical appearance of the peacock has taken, intra-sexual factors (between the males) had an influence. In any case, the end result is that a match between the signaler and the recipient, between the courtship display and the brain of the animal observer, is crucial for successful mating and procreation.

Honest Signals of Health in Nature: Handicap Principle in Biology and Art

Physical and mental effort, metabolic energy, muscle strength, immunocompetence, and high maintenance costs are required to display a perfectly healthy body to attract a mate for procreation. Having the elaborate appendages, which need to be displayed, takes a toll on the male animals and for that reason Zahavi suggested that honest signals carry a handicap (Zahavi, 1975, 1997). Only the strongest males can maintain a front that lures females. His theory has been debated and discussed by others and is now widely supported (Grafen, 1990). The costs of maintaining physical attributes that showcase fitness qualities are of and of themselves signals of genetic quality, the kind that maximize survival.

In essence, not only do the elaborate appendages hinder survival of the individual male, possessing them carries costs that are detrimental to health in the long run. Thus, male animals generally have lower life expectancy than females. Male big horn sheep butt heads with such force that the resounding head collisions are heard for long distances. But such battles cannot be maintained by the same ram year in and year out. The thick skull can absorb the impact for a long while until one ram collapses. The surviving ram wins the right to procreate with the females of the herd and thereby increase his progeny. Winning is physically costly.

Generalizing to art aesthetics/beauty, the greater the investment in the skillful execution of an artwork, the more it reflects favorable artistic genetic qualities, and the more likely it is to trigger aesthetic reactions in the viewer. The aesthetic response and the genetic qualities assessment pathways are assumed to share the same neural circuitry. Obviously, the artist is not promoting personal interest in procreation and attraction of a mate through the work. In producing the artwork, the artist is not “putting” the aesthetics into it; rather the work triggers the aesthetic reaction in the brain of the viewer.

The overall physical health of the artist is independent of the artistic cognitive abilities, although under some conditions it could shape the artwork (e.g., eye health conditions in some artists in the school of Impressionism). Countless renowned artists with serious health issues produced universally regarded, time-transcended valued artworks, among whom are Goya, Monet, Van Gogh, Mozart, Beethoven, and Schubert, to mention but a miniscule few (Zaidel, 2015b). It is the artistic cognition that is put on display and, ultimately, what is assessed by the viewer is the artistic genetic quality.

Considered within a biological and evolutionary framework, humans would not experience aesthetic reactions in the first place if there were no adaptive value to them. To wit, early on, both newborns and young children demonstrate selective response to beautiful faces (Bascandziev & Harris, 2014; Dion, 1973; Langlois, Ritter, Roggman, & Vaughn, 1991) attesting to the biological underpinning of the response.

Human Aesthetic/Beauty Response: Biological Roots and Evolutionary Co-option

Humans see beauty in the peacock's raised tail, its colors, iridescences, shades, and elegant crown, while peahens see an opportunity to inspect the peacock's health status. The brain of the observer limits what is sensed, perceived, and contemplated. Elliot Gould and Elisabeth Vreba developed the idea of co-option and labeled it exaptation: a structure or function originally arising to serve one biological purpose evolves further through environmental, physiological, and neural constraints to serve another function (Gould & Vrba, 1982). Here, it is argued that neural pathways that originally evolved to assess genetic qualities for mating and procreating have co-opted in the human brain to support nonbiological entities such as art and the aesthetic/beauty reactions to it. In human cultural existence, art has become a critical mode of social communication, symbolic expression of group unity, and display of genetic talent (Zaidel, 2017, 2018).

By inference, humans judge what they consciously think is artistic virtuosity but what enters the judgment formula without awareness is assessment of the artistic genetic quality. The assessment of health is a conserved trait inherited from animal ancestors, meant to serve a particular function for animals, but in humans it metamorphosed into an aesthetic/beauty response; that is, the response has co-opted to serve something immensely useful to humans, specifically the attentional honing to the message emanating from the source.

Attention-Attraction and the Aesthetic/Beauty Response

An important aspect of the genetic fitness display is that it is strategically organized to attract attention. This aspect is factored into the logic of the display as a whole and it, too, has been biologically preserved in humans (minus procreation needs). Universal principles of attention are so basic and advantageous to survival that it is reasonable to assume that they would be incorporated into behaviors targeting species procreation.

Neural systems supporting attention have formed early on in biological organisms. Attentional channeling of resources optimizes successful perceptual and cognitive assessment of the source's signals (Mangun, 2012). Detecting objects, sounds, vibrations, touch, smells, taste, and minute changes in the environment is crucial. Slight alteration in the surroundings could determine life or death, eating or being eaten, being unmasked or hidden, and so on. Similarly, species survival depends heavily on attention-attraction to animals' mate selection displays, an extension of basic alertness since it is critical for successfully choosing the best mate.

Humans no longer need dedicated neural resources for prey detection given their capacity to control and modify their habitat for protection; unlike animals, humans are famously highly adapted to new terrain, weather, and food sources through their mechanical and technological skills. Moreover, most humans no longer share the same environmental niche with animals. The attentional system was modified through evolutionary pressures to serve human-unique survival needs, and the human aesthetic response could be viewed as an extension, a co-option, of the strong biological need to draw notice to mating displays.

Indeed, myriad sources unrelated to obvious genetic showcasing trigger aesthetic responses. What triggers our heightened aesthetic response to the rising full moon, sunsets over the Pacific Ocean, shades of red in autumn tree foliage, drops of rain on waterlily-filled ponds, fire sparks in shooting volcanoes, flights of hummingbirds, or the iridescent colors in a peacock's tail? And conversely, what lessens our aesthetic response when the same full moon is viewed at zenith, when torrential rains hit the ground, or when freshly fallen snow on city streets is trampled upon by cars and pedestrians? Such considerations are contemplated by the Japanese school of aesthetics, Wabi-Sabi, which considers aesthetic response to imperfect, so-called ugly things (Koren, 2008). In all of these conditions, attention-attraction to the signals emanating from the source is the critical element: the signals attract attention, much as when the peacock's display draws the peahen's attention (Zaidel, 2015a).

Biological Aesthetics: Pleasure Versus Attention-Attraction

In evolutionary terms, choosing and displaying for the purpose of procreation requires attention, concentration, energy, and efficiency. With animals, the role of pleasure in this whole endeavor is unknown. Some published studies of visual art evaluation (paintings) have reported increased activation in the "reward pathway," which encompasses a so-called "pleasure center" (Aharon et al., 2001; Ishizu & Zeki, 2011). The pathway was originally uncovered in rats, in whom pleasure was inferred but not objectively verified (Berridge & Kringelbach, 2013, 2015). The occasional finding of increased brain activation in these areas in humans has suggested that pleasure is involved in the aesthetic evaluation of art but this inference has been challenged (e.g., Ticini, 2017), and even on the face of it, does not hold much weight.

Thus, the subjective feeling humans become aware of sometimes upon experiencing aesthetic reactions may not have emerged from inherited neural pathways controlling mate selection. Indeed, one would have to wonder, why pleasure? Arguing that the biologically conserved system from whence aesthetic reactions emanate has been preserved for the sole purpose of generating pleasure is highly tenuous. Rather, it is more reasonable to suppose that the occasional and transient nature of pleasure associated with some aesthetic reactions is a secondary event controlled by separate neural pathways. The human-specific aesthetic response itself likely rests on evolutionary modification of the biologically tuned attentional system.

Biological Aesthetics of Music

Music is an art form that is ubiquitously present in human cultures and this suggests a basis of inherited biological foundation for composing and performing it. Indeed, the human ear structure and the neural auditory system have origins in distant phylogenetic species, possibly emerging with fish (Manley, Popper, & Fay, 2004). With most animals, deciphering sounds is constrained by the environment and the functions subserved by those sounds, even while there is conservation of brain areas responding to music across widely divergent species such as crocodiles, birds, and humans (Behroozi et al., 2018). Similarly, human neural brain organization and functionality are likely to have shaped the upper limits of hearing the sounds of language and music (Ayala, Lehmann, & Merchant, 2017; Baumann, Petkov, & Griffiths, 2013).

Given conservation of sensory auditory neural systems, we need to explore the biological ancestry to gain an understanding of the human response to music. The principal reasons why animals produce sounds include declarations of territorial boundaries, predatory warning calls, physical strength displays, information sharing, and mate selection displays. Bird songs have been studied by far the most and provide a model for insights into human and animal communication (Knight & Lewis, 2017; Rothenberg, Roeske, Voss, Naguib, & Tchernichovski, 2014). Birds sing to signal their territory, bond with mates, declare affiliation, and display fitness strength; additional reasons remain to be uncovered. A clear sex difference in song production has been observed: males sing to attract mates while females rarely sing, and this male dominance suggests an early (evolutionary) sexual role of sound formation skills. Songs are learned through mimicking after birth. Learning from their conspecifics is achieved during a period of growth when brain plasticity mechanisms are functional; early isolation from conspecifics produces distorted songs (Nottebohm, 2005).

However, a driving evolutionary force in shaping the human brain is language communication, the antecedents of which have a long evolutionary history traced to nonhuman primates (Aboitiz, 2018), and to the adaptive strategy of social bonding and group belongingness (Zaidel, 2018). At the same time, our reactions to music are biologically linked to other animals' intra-species communication and mating fitness signals (Zatorre & Peretz, 2001). Indeed, human musical compositions share elements produced by birds, whales, frogs, and numerous other animals, despite evolutionary paths that diverged from our ancestors millions of years ago (Fitch, 2015; Honing et al., 2015). The fact that young babies and children react to music early on without any instruction, and the ubiquitous presence of music throughout human societies both attest to its strong biologically based social, emotional, and aesthetic appeal (Mithen, 2009).

Human brain neuroanatomy supporting the sounds of language specialization, asymmetrically emphasizing the left hemisphere, has been evolving in nonhuman primates (Aboitiz, 2018; Cantalupo & Hopkins, 2001; Hopkins et al., 2017), whereas musical processing, an art expression, involves activation of neural systems in both hemispheres, and musical compositions, too, lack robust asymmetrical hemispheric control (Zaidel, 2015b). The two human abilities, language and music, share neuroanatomical structures but are not organized similarly in the brain, although both have social and participatory communicative functions.

Music's Emotional Pleasure and Communication

In addition to the aesthetic/beauty issue, humans experience a variety of emotions evoked by music, including sadness, relaxation, melancholy, elation, excitement, arousal, and more. Pleasure is the most discussed in this context (Zatorre & Salimpoor, 2013). We verify the emotions explicitly ("I enjoy this music," "I love this music," "this music is beautiful," etc.) (Schaefer, 2017). Subjectively, peak emotions and pleasure with music are experienced as physical bodily chills, thrills, shivers, goosebumps, known scientifically as piloerections (Goldstein, 1980; Panksepp, 1995). How and why piloerections are triggered is not currently understood. Moreover, there is great variability in the response itself; some report not experiencing them at all while still reporting subjective pleasure.

The sympathetic branch of the autonomic nervous system controls the contraction of the skin muscles involved in piloerections (Benedek & Kaernbach, 2011). Anatomically, smooth muscles underlying skin hair follicles are stimulated by the sympathetic branch. In the brain, the autonomic system is controlled by the hypothalamus, which also controls heart rate, respiration, digestion, body temperature, and other functions normally not under voluntary control. The response of piloerections is involuntary in both humans and animals, whether it is caused by fear, flight, coldness, or stress. The relationship between the hypothalamus and music is not clear cut. However, this brain structure is part of the limbic system, which is known to be involved in emotional reactions, and receives input from widely distributed neuroanatomical structures in the cerebral cortex and brain stem.

Exploiting the deeply rooted biological, anatomical, and neural circuits to create and enjoy music is a natural step in the evolution of human social culture. Initially, early humans emerging in Africa, *Homo sapiens*, could easily have discovered that animal mimicry through modulation of guttural throat sounds, tongue clicks, and whistling provided the right kind of camouflage for successful hunting or scavenging (Zaidel, 2017, 2018). The same could be assumed for symbolic sound-making, through throat or instrumental production, by *Homo neanderthalensis* in Europe (d'Errico et al., 2017; Hoffmann, Angelucci, Villaverde, Zapata, & Zilhão, 2018), and, by extension, possibly even by *Homo erectus*, who dispersed away from Africa well over a million years earlier than *Homo sapiens*. Responding to these sounds meaningfully in musical rhythms, beats, and harmony with percussion on stones, wood, leather, bones, or through whistling with plant material (leaves, reeds) would have been a natural endeavor in the distant past (Zaidel, 2015b).

Although physical material artifacts of music-making are missing from the archeology of the very early hominin epochs in Africa, emerging only ~40,000–30,000 years ago in Europe, vocally produced nonlanguage, purposeful rhythmical human sound-making could nevertheless have been practiced for symbolic purposes denoting social unity and cohesion (Zaidel, 2017). The archeological record shows consistent socially based group living dating all the way back to ~300,000 years ago (Brooks et al., 2018; Potts et al., 2018; Tooby & Cosmides, 2016). A human musical chorus of voices could easily have included all group members regardless of social hierarchy, age, or sex. Aesthetic/beauty issues would have been secondary because they would have emphasized individual displays of talent, potentially triggering competition among individuals (jealousy and conflict?), instead of whole group displays (Zaidel, 2018). It is parsimonious to assume that the primary reasons were the group's survival as a cooperative socially oriented unit. The fact that this strategy was successful can be seen in the eventual spread of *Homo sapiens* to the rest of the world. Currently, we do witness individual musical composers, single instrument players, and a range of vocal singers displaying their virtuosity because the dynamics of flourishing societies have cultural norms that allow such exhibits. Humans have become resourceful with regard to survival and can afford to practice expanded cultural repertoires.

Conclusion

The human aesthetics/beauty response has been linked to conserved biological pathways inherited from the animal ancestry, particularly to mate selection strategies. It plays a role in the arts, commercial advertisement, decision making, career paths, jury selection, and mate attraction, and is also triggered by scenery, food, and parenthood. The broad range of beauty triggers in human existence suggests the response has been co-opted and modified to blend into the cultural reality of human survival practices. It has an evolutionary adaptive purpose.

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