On The Evolution of Human Aesthetic Preferences.

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How can we imagine that an inch in the tail of the peacock, or ¼ inch in that of the Bird of Paradise, would be noticed and preferred by the female? Alfred Wallace, letter to Charles Darwin, March 1868.

In regard to sexual selection. A girl sees a handsome man, and without observing whether his nose or whiskers are the tenth of an inch longer or shorter than in some other man, admires his appearance and says she will marry him. So, I suppose, with the pea-hen ..... Charles Darwin, letter to Alfred Wallace, March 1868.

Introduction

The archaeological record of the last Ice Age, particularly after about 40,000 years ago, documents the emergence of clearly symbolic behaviour, including burials that were furnished with grave goods, the invention of parietal and portable representational art, the use of items of body ornamentation and possible instances of numerical or calendrical notation (Pfeiffer, 1982). This kind of material cultural evidence has informed and stimulated the discussion of the evolution of modern human cognitive abilities, but there is also an important aesthetic dimension to human culture, and as Kaplan (1992) has emphasised, evolutionary explanations of human aesthetic preferences benefit from integrated approaches that consider both cognitive and emotional responses. On both theoretical and empirical grounds it is likely that human emotional adaptations evolved much earlier than strictly symbolic capacities, given that 99% of the five million year timespan of hominid evolution preceded the emergence of material evidence for symbolic behaviour. Thus the study of human aesthetic preferences may provide a window into an extensive epoch in the early evolution of the human psyche.
In this paper I review some human visual aesthetic preferences that may have originated in our species’ distant evolutionary past. These preferences include evolved responses to natural landscapes, symmetry preferences, and criteria of facial attractiveness. In the discussion that follows I employ a very general definition of aesthetics, best summarised as "mental appreciation of the shape or embellishment imposed on raw materials" (cf. Dissanayake, 1992), in which the term "appreciation" primarily denotes an involuntary emotional response to a stimulus, rather than the deliberate intellectual stance adopted by the modern professional or philosophical aesthete.

Landscape Preferences and the Hominid Environment of Evolutionary Adaptiveness

An innate human preference for visual landscapes that have properties resembling those of savanna habitats (i.e. low-relief, sparsely-wooded tropical grasslands: Figure 1a & b) has been attributed to selection pressures operating during early human evolution (Balling & Falk, 1982; Orians & Heerwagen, 1992). According to Orians and Heerwagen, present-day humans express a rapid and often unconscious affective response to those general properties of a landscape that are perceived on initial visual encounter. Preferred landscapes are those containing features indicative of environmental conditions favourable for survival, such as an abundance of subsistence resources or a minimal threat from predators. The preference for savanna-style visual landscapes is most strongly expressed in children (Balling & Falk, 1982), and is also manifest in the deliberate design of artificial landscapes as exemplified by modern (i.e. post-Renaissance) ornamental parks and gardens (Kaplan, 1992). A more specific hypothesis of
landscape preference stems from "prospect-refuge theory", which predicts that within a given landscape preferred locations are found at interfaces between prospect-dominant and refuge-dominant areas (Appleton, 1996). These vantage points combine unimpeded visual prospects with a ready opportunity for concealment and/or withdrawal to a safe refuge. Thus a treeless landscape is less visually attractive than a habitat containing isolated trees that can provide opportunities to hide or escape from potential predators.

Exponents of the human preference for savanna-like habitats have reasoned that the human environment of evolutionary adaptiveness (EEA) was located in the Plio-Pleistocene savannas of sub-Saharan Africa. It has been argued that habitual occupation of the savanna biome by *Australopithecus* and early species of *Homop*rovided an extended period of selection for the reinforcement of intuitive preferences for certain topographic, botanical and faunal features of the savanna landscape (cf. Orians & Heerwagen, 1992: 556). However, this scenario of human evolution is over-simplified, and there is an increasing consensus among palaeoanthropologists that there is no single unitary environment to which earlier human species were optimally adapted (Foley, 1996). *Ardipithecus ramidus* and *Australopithecus anamensis*, the earliest known hominids, show morphological adaptations to arboreal substrates (White et al., 1994; Leakey et al., 1998) and the fossils of *Ardipithecus ramidus* have been recovered from depositional contexts characteristic of closed canopy woodland rather than open savanna (WoldeGabriel et al., 1994). Furthermore there is also an extensive and more recent history of human occupation of non-savanna biomes, especially after 1.8 million years ago when species of *Homo* first appear in higher latitude regions of Asia and Europe.

Evidence of heterogeneity in hominid landscape preferences has been sought in studies of the geological and ecological contexts within which hominid fossils
have been discovered, in an attempt to delineate ecological differences between hominid species (Behrensmeyer, 1978; White, 1988). There is a substantial and difficult taphonomic problem here: are the habitats that are conducive to the deposition and preservation of hominid fossils representative of the environments to which the hominids were originally and optimally adapted? White’s (1988) analysis of the relative frequencies of *Homo* and *Australopithecus* fossils in different African palaeoenvironments failed to confirm earlier suggestions that *Homo* fossils were relatively more common in river bank and lake margin settings. However, most of the East and South African Pleistocene hominid sites have palaeoenvironmental profiles indicating a mosaic habitat, with a mixture of flora and fauna that are individually adapted to open grassland, woodland and proximity to water. This provides indirect support for the prospect-refuge theory of human landscape preference, as the palaeoenvironmental evidence would be expected to show a mixture of habitat types if hominid occupation sites were preferentially located at habitat interfaces.

Thus if there is an evolved human psychological preference for savanna habitats this is unlikely to have been inherited as a phylogenetic legacy from a much earlier (i.e. australopithecine) phase of human evolution. The palaeoecological evidence, though sparse, suggests that Lower Pleistocene hominids favoured either closed woodland (*Ardipithecus*) or mosaic habitats (*Australopithecus* and early *Homo*). Furthermore, in living primates there are instances of divergence of substrate and habitat preference between closely-related species (for instance, both arboreal and terrestrial species exist within each of the genera *Cercopithecus* and *Macaca*), suggesting that evolved environmental preferences in primates are typically species-specific adaptations rather than plesiomorphic traits inherited by all members of a genus. This raises the possibility that the savanna landscape preference that characterises modern humans arose relatively recently, perhaps coinciding with the emergence of anatomically modern *Homo sapiens*. One model of the origin of anatomically modern humans places the crucial speciation event that gave rise to our species in sub-Saharan Africa, at about 100,000 years ago (Stringer & Andrews, 1988). It is therefore possible that the preference for savanna habitats emerged when modern humans were confined to these regions of Africa, prior to their expansion to other regions of the world during the Upper Pleistocene.

**Symmetry Preferences**
Geometrical symmetry is widespread in nature and in human culture. A feature of both the natural and cultural realms is that symmetry of form is frequently over-determined in relation to functional necessity: that is, organisms and artefacts often appear to be more symmetrical than is strictly necessary for the purposes of efficient mechanical design. In animals, the apparent regularity of bilateral symmetry is sometimes literally skin-deep: dissection reveals that the thoracic and abdominal organs of humans (and other vertebrate animals) are profoundly asymmetrical. In like fashion, artefacts often exhibit patterns of symmetry that are not dictated solely by technological considerations (Wynn, 1995, 2000; Kohn & Mithen, 1999).

A large body of experimental evidence supports the hypothesis that many species of animals use symmetry in the external appearance of conspecifics as a visual or tactile criterion in mate selection. Symmetry preferences may emerge either as an unintentional by-product of the evolution of visual shape recognition mechanisms (Enquist & Arak, 1994; Johnstone, 1994) or because symmetry is an effective and easily perceived measure of genetic quality (Møller, 1990; Parsons, 1992). As both sides of a bilaterally symmetrical animal are usually products of the same genetic code, small deviations from symmetry between the left and right sides of an organism serve as a proxy measure of how faithfully the animal’s genotype has been expressed during its development. Individual animals differ in their degree of random departures from symmetry because they differ in their ability to execute developmental programs accurately when challenged by environmental stress: symmetry is thus a sensitive indicator of the genotype’s ability to canalise development and of its resistance to environmental stress. The morphological ideal of symmetry is easily conceptualised, and even small deviations from the ideal are therefore detectable and measurable by simple perceptual systems.

Visually striking external weapons and ornaments serve as effective "honest advertisements" of an animal’s phenotypic quality. Single ornaments (e.g. horns in rhinoceroses) are placed centrally, and paired display structures (e.g. antlers in deer and tusks in elephants) are positioned with sufficient proximity to each other to facilitate rapid visual assessment of their degree of symmetry in size and shape. Selection of mating partners places secondary sexual traits or ornaments under strong directional selection, and an additional effect is that the symmetry and the size of an ornament become positively intercorrelated, that is individuals with the largest ornaments tend also to be more symmetrical (Møller, 1990). Thus individuals with superior quality or condition can advertise their status by developing both large and symmetrical traits, and
since this is a strategy that inferior animals are unable to mimic these structures serve as "honest" markers of fitness (Zahavi & Zahavi, 1997).

In male non-human primates the enlarged upper canine teeth serve as display organs, and the degree of symmetry between the size of the right and left side canine teeth is correlated with the intensity of sexual selection (Manning & Chamberlain, 1993). In strongly sexually dimorphic primate species, such as the western lowland gorilla, the male animals with the largest canine teeth are also those with the most symmetrical teeth (Manning & Chamberlain, 1994), indicating that for these animals there is intraspecific selection for both size and symmetry in the canine teeth. Hominid species, in contrast, have reduced canine teeth that do not project significantly beyond the occlusal plane, yet early hominids of the genera *Ardipithecus*, *Australopithecus* and *Paranthropus* show marked sexual dimorphism in body size, an attribute which is consistent with elevated levels of inter-male competition. Canine reduction in hominids coincides with the appearance of bipedal posture and locomotion, and it is possible that active bipedal displays replaced static canine displays in agonistic encounters between early hominids (Jablonski & Chaplin, 1993).
Unfortunately there are too few sufficiently well-preserved fossil specimens to test for the possible effects of sexual selection on the symmetry of canine teeth of early hominids, but from about 2½ million years ago an increasingly rich archaeological record emerges providing an opportunity to examine symmetry preferences in the manufacture of stone tools. As Wynn (1995, 2000) has shown, simple worked cores and flaked stone tools of the Oldowan (Mode 1) cultural repertoire do not incorporate a principle of symmetry, but in Acheulian bifacial (Mode 2) production sophisticated symmetries in three dimensions are achieved (Figure 2). Acheulian handaxes are clearly over-determined in their symmetry of outline in relation to their design and use as cutting or chopping implements. This implies that in addition to a strictly utilitarian role they may have served as display items, perhaps as signs of the perceptual and productive skills of their makers, or simply as aesthetically satisfying objects (Kohn & Mithen, 1999). This conjecture that these artefacts are display items is testable because, as with visually prominent organic weapons and ornaments, we would expect a positive correlation between the size and the overall symmetry of the artefact. The correlation arises because both large size and symmetry enhance

**Figure 2(a):** Example of an Acheulian (Mode 2) tool: an ovate handaxe from Upper Bed II, Olduvai Gorge. The tool exhibits bilateral symmetry in three planes: in plan view (left), in profile (right), and in transverse cross sectional planes (not shown). Scale bar is 10 cm. Drawing by the author, after Leakey (1971).

**Figure 2(b):** Example of an Oldowan (Mode 1) tool: an end chopper from the ‘Zinjanthropus’ level in Bed I, Olduvai Gorge. No concept of symmetry is embodied in this tool. Scale bar is 10 cm. Drawing by the author, after Leakey (1971).
the visual impact of a handaxe, so the most impressive artefacts are those which excel in both attributes. As handaxes are manufactured by reduction from a large core it is exceedingly difficult to manufacture large and symmetrical items - symmetry is only achieved by removal of stone - and a large symmetrical axe will therefore serve as an 'honest' advertisement of its maker's knapping skills.

Although I do not have access to appropriate data on the symmetry of Lower Palaeolithic artefacts I have measured the symmetry of a large sample of British Neolithic stone axes for which the cross-sectional shapes have been published (Adkins & Jackson, 1978). Circumstantial evidence suggests that these artefacts had a significant display value - they were sometimes made on precious raw materials and are distributed many hundreds of kilometres from the source of stone, they were frequently polished on all surfaces and not simply on the cutting edge, and they are often discovered in an unused condition and are sometimes clustered in hoards and in votive deposits. The cross-sectional asymmetry of a sample of 333 Neolithic axes recovered from the River Thames in southern England shows a small but significant negative correlation with the length of the artefact, as expected if both size and symmetry of outline form were preferred criteria. Small axes may, but need not be symmetrical, but large axes are much more likely to have a symmetrical cross section (Figure 3).
Figure 3: The relationship between cross-sectional asymmetry and length in Neolithic stone axes. Asymmetry is measured from cross-sectional profiles as the deviation in degrees of the axis of maximum thickness from a line drawn at right angles to the axis of maximum breadth. The axis of maximum thickness is defined as the line connecting the two points where lines that are parallel to the axis of maximum breadth make tangential contact with the cross-sectional outline of the axe. Asymmetry is negatively correlated with the length of the axe: $r = -0.24$, $n=233$, $p < 0.01$

Mithen (1997) has argued that the archaic minds of pre-modern hominid species had 'domain specific' intelligence in which the modules concerned with interacting with the natural world were essentially isolated from the mental modules employed in the manufacture and use of artefacts. The presence of patterns of symmetry in Lower Palaeolithic artefacts that mimic those found in biological weapons and ornaments suggests that aesthetic preferences, at least, may be less constrained by domain specificity than has been argued in the case of more explicitly cognitive properties of the evolving human mind.

**Facial Attractiveness**

It is likely that humans and non-human primates share evolved mechanisms that specialise in facial recognition and in the interpretation of facial emotional expressions. In humans these mechanisms for processing visual data from
facial configurations are augmented by shared, possibly species-specific, preferences in facial attractiveness. While non-human primates are similar to humans in some aspects of their face recognition mechanisms (e.g. Phelps & Roberts, 1994) it is not yet clear whether facial attractiveness is an important criterion of mate selection in primates, although the vivid and often sexually dimorphic facial colouration of guenons and mandrills is believed to result from directional sexual selection (Kingdon, 1980).

A large amount of research has been published on determinants of facial attractiveness in humans, but many studies have been restricted in scope, for example evaluating exclusively preferences for female faces or confining their analyses to western (Caucasian) populations. As with landscape preferences, differential interest in attractive adult female faces emerges early in the first year of infancy implying that the preference for attractive faces is more likely to be an evolved response than a learned behaviour (Langlois et al., 1987). There is also a significant degree of cross-cultural agreement between tests of ratings of facial attractiveness conducted in populations of different ethnic backgrounds (Jones et al., 1993; Perrett et al., 1994). Taken together this evidence disproves the argument that criteria of physical attractiveness are determined by arbitrary cultural conventions.

What are the structural characteristics of human faces that influence judgements of facial attractiveness? Artificial facial images constructed from composites of a sample of different faces are rated as being more attractive than the individual source images (Symons, 1979; Langlois & Roggman, 1990). This finding of a preference for a stereotypical average has been cited as evidence for the effect of stabilising selection on facial shape, but the computer graphical processing of images to generate a sample average increases facial symmetry and eliminates facial irregularities, and this "smoothing" effect in itself makes facial composites appear more youthful (Burt & Perrett, 1995). Males especially show heightened preferences for younger female faces, and it is therefore difficult to ascertain whether "averageness" per se is attractive (Alley & Cunningham, 1991). Individual faces that are rated as highly attractive are in fact not average but depart from the sample and
population mean in predictable ways, and artificial exaggeration of distinctive differences from the average face through automated caricaturisation enhances facial attractiveness (Perrett et al., 1994). In Perrett et al.’s study of Caucasian and Japanese subjects, attractive female faces in both populations had a thinner lower jaw, shorter lower facial height, higher forehead and relatively larger eyes (Figure 4). These characters are neotenous in humans and therefore contribute to a youthful facial appearance in adults (Jones, 1996).

Figure 4: Outline of a composite face constructed from the average of 60 Caucasian females (redrawn from Perrett et al., 1994). Arrows indicate the vectors of change of topographical landmarks when the average face is morphed onto the mean of the 15 faces with the highest attractiveness ratings. These vectors show that the stereotypical attractive face has a thinner lower jaw, reduced lower facial height and a higher forehead than the population average.

Human facial preferences may have a deep evolutionary history. The morphological characters of the female face that influence attractiveness are also those which have been subject to directional evolutionary change during human evolution, particularly during the Pleistocene evolution of the genus Homo, and they are part of a suite of uniquely derived morphological characteristics that distinguish Homo sapiens from all other hominids. It is therefore possible that current human facial preferences are founded on a legacy of directional selection for characteristics that are important in the human specific-mate recognition system. This hypothesis can only be tested indirectly on the skeletal remains of fossil hominids (faces do not fossilise, and forensic methods of reconstructing faces from skeletonised remains are inherently unreliable).

It is also noteworthy that neotenous facial proportions elicit protective and nurturing behaviour in human caregivers (McCabe, 1988), and the same effect can be observed in other mammals (Lorentz, 1971). Elicitation of parental care may be of heightened importance to humans because of the extended period
during which human offspring are dependent on the support of adult kin. Criteria of human facial attractiveness may therefore reflect a generalised mammalian preference for neotenic facial forms, and it is interesting to note that human standards of attractiveness are frequently applied to animals and may be implicated in the morphological changes that have accompanied the domestication and selective breeding of animal species (Clutton-Brock, 1981).

Conclusion

This short review has only examined one sensory modality - vision - and discussion has been limited to three arenas within which visual aesthetic preferences appear to have an evolutionary origin. Evolved responses to aspects of the visual environment appear to be a palimpsest of adaptive strategies of greater and lesser antiquity (Table 1).

Table 1: Possible Origins and Functions of Human Aesthetic Preferences

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<th>Preference</th>
<th>Hypothesised Origin</th>
<th>Postulated Function</th>
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<td>Anatomically modern <em>Homo sapiens</em></td>
<td>Foraging and defence</td>
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<tr>
<td>Symmetry in Organisms and Artefacts</td>
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<tr>
<td>Facial Attractiveness</td>
<td>General mammalian preference, perhaps increased in importance in early <em>Homo</em></td>
<td>Mate selection, and elicitation of nurturing behaviour</td>
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Landscape preferences are *a priori* likely to be species-specific, and the "savannah" preference documented for modern humans can be interpreted in the light of the "Out of Africa" model which posits a recent sub-Saharan origin for our species. Symmetry preferences may have originated in mechanisms that evolved for monitoring phenotypic quality in conspecific mates: such mechanisms are extremely widespread in nature, and the fact that the symmetry preference is easily transferred to items of material culture that have semiotic value suggests that the preference may serve a domain-general function in humans. Facial attractiveness may reflect a generalised mammalian preference for neotenic facial forms, but selection for neotenous faces appears to have been enhanced in early *Homo* and was sustained during the evolution of Middle
and Upper Pleistocene members of our genus.

References


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