



KEYWORDS: *Aesthetics – Co-evolution – Rock art – Sexual selection – Motif – Technique*

EVOLUTIONARY AESTHETICS AND SEXUAL SELECTION IN THE EVOLUTION OF ROCK ART AESTHETICS

Marco Antônio Corrêa Varella, Altay Alves Lino de Souza and José Henrique Benedetti Piccoli Ferreira

Abstract. This theoretical proposal applies evolutionary aesthetic, animal signalling and sexual selection to understand our artistic cognition, especially rock art aesthetics. Iconographic motifs, universally found in rock art, indicate which set of pre-artistic aesthetic psychological bias has been co-opted to catch the viewer's attention. The co-evolutionary process of sexual selection could have shaped the design features of both rock art images and their aesthetic cognition by conferring mutual benefits on both producers, via manipulation, and receivers, via information extraction. We show some strategic techniques identified in rock art and art that indicate the occurrence of this co-evolution between producers and receivers.

Introduction

Much has been said about the evolutionary aspects of human artistic expression (Coe 2003; Diamond 2006; Dissanayake 1988, 1992, 2000a; Dutton 2009a; Eibl-Eibesfeldt 1989a; Miller 2001; Pinker 2002; Souza 2004). The discussion is essentially focused on whether the *making* of art, more specifically music, is a product of artistic mental adaptations or *only* a by-product of pre-existing capacities in the human mind. The issue, however, is not one of attempting to dignify things we like, such as art, by turning them into biological adaptations (Dutton 2009a), because both exapted by-products and proper adaptations originate from ancient adaptations. Andrews et al. (2002) showed that even the exaptationist program requires considering and testing adaptationist hypotheses. That is why we need to combine the study of the precursors of adaptations and ancestral adaptive values when studying the origins of art.

Also the question is not only about art-making alone, because art-making and appreciation have co-evolved: even those who perceive and appreciate art, non-artists so to speak, have artistic aesthetics capacities and enjoy being with and evaluating works of art (Funch 1997; Grinde 2000; Huron 2001). Therefore, what is needed is a demonstration of how our artistic appreciation emerged from ancient non-artistic aesthetic appreciation, co-evolved with art production, and of how strong were the selective pressures acting

on this new artistic aesthetics. As Dutton (2009a) says: 'Darwinian aesthetics will achieve explanatory power neither by proving that art forms are adaptations nor by dismissing them as by-products, but by showing how their existence and character are connected to Pleistocene interests, preferences, and capacities' (Dutton 2009a: 96).

Given the importance of aesthetic experience for understanding art, and given the importance of evolution for understanding human nature, in particular with respect to rock art expression and appreciation, our aims are twofold: first, to clarify the role of evolutionary explanations for human behaviour by resolving many common misinterpretations, seeking to open an opportunity for a genuine dialogue between fields; and second, to present a theoretical proposal elucidating ways in which evolutionary processes might have shaped aspects of our artistic cognition involved in visual arts, especially rock art. We look to evolutionary aesthetics (Thornhill 2003; Volland and Grammer 2003) for its origins and to sexual selection (Dutton 2009a; Miller 2001) as its maintenance process.

We will begin by discussing how aesthetics can be studied from an evolutionary perspective, always elucidating what it really means to say that we have an evolved aesthetical psychology. Dutton pointed out that '... modern philosophers have been reluctant to connect aesthetic experience to any specifiable notion of human nature, or an empirical psychology that would

seek to discover it' (Dutton 2009a: 39). And Pinker (2002) has argued that the denial of human nature in modern intellectual life is an obstacle for appropriate understanding of the evolutionary contribution to the arts. Therefore we deal carefully with these two sources of resistance in order to open a real opportunity for dialogue between different fields and 'breach the gap between biology and philosophy, by showing it in a new light' (Volland and Grammer 2003: 5).

We will then present a suggestion as to how the iconographic motifs universally found in rock art can indicate which pre-artistic aesthetics psychological adaptations have been mostly co-opted to catch the viewer's attention in order to gain insight into the origins of visual art. The idea that there is a similarity between the appreciation of forms of nature and the appreciation of art forms is not new, as even Aristotle argued that all kinds of art are imitations of forms of nature. However, connecting these traditional ideas with recent evolutionary approaches to human behaviour can promote new ways of seeing the relationship between aesthetics and rock art.

Finally, we will show how sexual selection could have intensified the selective pressure upon the psychological mechanisms underlying rock art aesthetics by its co-evolutionary nature between image-makers and image-enjoyers. When both sides can gain fitness benefits, given enough time, over generations, co-evolution would generate new traits by exaggerating and diversifying ancient traits. We show some strategic techniques identified in rock art and recent art that indicate the occurrence of this co-evolution between producers and receivers, including ways of testing it. It is also essential to clarify misconceptions concerning the process of sexual selection for us to properly understand its power and implications (Miller 2003).

Evolutionary aesthetics

Evolutionary aesthetics (Eibl-Eibesfeldt 1989a; Grammer et al. 2003; Volland and Grammer 2003) is a field studying the evolution of the many psychological mechanisms that underlie the entire diversity of aesthetic experiences. Some authors have focused more on simple perceptual aesthetic bias (Eibl-Eibesfeldt 1989a; Ramachandran and Hirstein 1999) and some have focused on bias concerning people, animals, food and landscapes (Thornhill 2003). Either way, the whole spectrum of human aesthetic evaluation, from our enjoyment of beauty to our aversion to ugliness, as with pleasure and pain, is seen as a psychological guide to situations leading to survival and an increase in reproductive potential in ancestral environments. The experience of beauty is linked to enhanced fitness in human evolutionary history, while ugliness is just the reverse (Thornhill 2003). Note that aesthetic processing is conceptualised as a phenomenon on a psychological continuum with both positive and negative extremes. Thus, negative emotions such as aversion and disgust are just as much aesthetic emotions as are wonder and

elation.

Evolution is habitually thought of in solely physiological rather than psychological terms. It is not merely that evolution has shaped immune systems, digestive tracts, lungs and kneecaps. Evolution has also shaped our attitudes, dispositions, emotions and perceptions; in sum, complex cognitive functions including our aesthetic appreciation (Dutton 2009a). These are our psychological adaptations: evolved, domain-specific mental capacities that may include perceptual, cognitive, emotional, motivational, learning and motor control sub-systems (Andrews et al. 2002; Thornhill 2003).

As a distal historical explanation interested in universal physiological and psychological mechanisms, the theory of evolution does not imply that there is no need to formulate more recent historical or proximate theories anymore, nor that one type of theory is more correct or better than the other. Explanations focused on cultural or individual idiosyncrasies do not contradict evolutionary explanations (Ridley 1993), as long as they take into consideration that humans are animals with evolved psychological faculties rather than being blank slates (Pinker 2002). Evolutionary explanation provides one more kind of analysis, and in combination leads to a broader understanding of human phenomena.

Sometimes understanding the process of evolution is difficult because people often think that there is a contradiction between the process and the fact that humans do not think about the effects their art activity might have on the selection of their genes. We do not need to know that evolution has been selecting some genes that influence a phenotype and a behaviour that affects other minds in ways that enhance our fitness in order for natural selection to occur (Dawkins 1982). Selection is a cross-generational, blind, population level algorithmic process that consists of differential survival and reproduction by individuals because of differences in their phenotypic design with respect to their physical and social environments (Thornhill 2003). We are the only species that knows about evolution, but every living population evolves. We do not need to know the underlying logic or even all the benefits in terms of fitness to execute an effective instinctive activity. A spider does not need to know how and why its ancestor started building webs, nor anything formal about the engineering required to build it to do so (Alcock 2001).

There are two types of evolutionary historical causes: one deals with phylogenetic origins and is concerned with all ancestral precursors of a given trait; the other one deals with its maintenance, which is the ancestral adaptive value that explains how such a trait has escaped the hatchet of natural selection, that is, what advantage over which costs was conferred on those individuals who more strongly express such a trait. The origin and selection history of an adaptation are complementary and both are necessary to understand

the big evolutionary picture of any trait (Mayr 2004; Tinbergen 1963).

It is important to say that in evolutionary biology, in general, adaptation refers to goal-directed, functionally designed, phenotypic features (Andrews et al. 2002; Thornhill 1990, 1997; Symons 1992; Williams 1992). As Williams (1992) put it, an adaptation is the material effect of response to selection. An adaptation, then, is a phenotypic solution to a past environmental problem that persistently impinged on individuals for sufficient generations of evolutionary time and thereby caused cumulative directional selection, which, in turn, caused cumulative directional change in the gene pool. Evolutionary aesthetics elucidates the design of the universal psychological adaptations involved in aesthetic experiences by using the heuristics of Darwin's evolutionary theory.

Having a universal set of psychological adaptations involved in aesthetic experiences means that humans indeed have a species-specific concept of beauty (Eibl-Eibesfeldt 1989a; Grammer et al. 2003). This does not contradict the fact that individual and cultural variation exist because of two main reasons:

- (1) Evolutionary biologists (Mayr 2004) see species' traits not in a typological or essentialist way, but as population phenomena, which means that the exceptions do not easily disprove the general rule in the way they do in physics and chemistry. The fact that there are some people who do not like sweet tastes, choose not to have sex, or even commit suicide is not a proof against evolution, because (a) there is always individual variation in populations due to random mutations and re-combinations and (b) evolution occurs mostly by eliminating the relatively most unsuccessful rather than by selecting only the relatively most successful ones (Mayr 2004). So the fact that some people never look at art, get any pleasure from art, or even destroy art works does not indicate that there is no universal concept of beauty or art instinct: universality does not mean 'exactly the same in everybody's behaviour', but a 'similar underlying bias in most people's behaviour';
- (2) Also, our psychological adaptations are sets of biases and learning propensities open to specific aspects of the developmental and contextual environment. These vary across individuals and cultures, so the universal concept of beauty will have modified standards for different people or cultures; however, it will not be completely eliminated in most people (Thornhill 2003).

Pre-artistic aesthetic psychology

Up to now there is no satisfactory taxonomy of the proposed psychological adaptations underlying the diversity of aesthetic experiences, those cognitive mechanisms focused on different aspects of our ancestral environment used for aesthetic judgments,

prior to art. Thornhill has proposed a list of ten different aesthetic adaptations. He points out that there is no clear objective way to delimit the aesthetic domain in Darwinian terms, so he uses historical precedent in the field of aesthetics as a criterion for defining the types of experiences to which beauty is applied: '... when aestheticians show great interest in a domain of experience, it is because of the power of aesthetic feelings in the domain' (Thornhill 2003: 27). He suggested that there could be adaptations for the aesthetic valuation of: (1) landscape features, (2) non-human animals, mostly for consumption (fish, ungulates, certain rodents and birds) or safety from predators (un-alarmed birds or ungulates calmly grazing), (3) acoustical behaviour of non-human animals, (4) daily or seasonal environmental change cues, (5) human bodily form, (6) status cues, (7) social scenarios, (8) skilfulness, (9) food and (10) ideas (intellectual beauty detector).

All of these aesthetics adaptations predate the onset of any artistic expression. Heyd and Clegg (2004) say that there are some preconceptions about aesthetics in that sometimes it is supposed that aesthetics necessarily has to do with art. But as they say, the diversity of aesthetic experiences covers many more situations than art appreciation itself. And Morris states that 'the aesthetic urge in *Homo sapiens* is not some recent refinement of civilisation, but part of an ancient, deep-seated need of our species' (Morris 1998: viii).

It is important to note that the list given by Thornhill (2003) is not the final word on this topic, but on the contrary, it is just the beginning of the investigation of psychological specificities underlying each human aesthetic experience. Many important aesthetic experience domains are missing, such as cues of neoteny (infantile traits), human voices, flowers, predators, insects, fire, water etc. The adaptationist approach can also be useful in drawing the boundaries of the cognition involved in aesthetic modules at its natural joints.

Adaptations are our sole source of information about the forces of selection that were actually effective in designing phenotypes over the course of evolutionary history. Note that the data encoded in the design of an adaptation concern the environmental features that caused differences in individual reproductive success during the evolution of the adaptation. This is just another way of stating that adaptations have stamped in their functional designs the selective forces that made them (Andrews et al. 2002; Thornhill 2003).

Therefore, the adaptationist program is to be used by evolutionary aesthetics to test whether those ten forms of aesthetic valuation, and many other perceptual ones as proposed by Ramachandran and Hirstein (1999), have typical characteristics of most adaptations, such as: special design, beneficial effects, high efficiency, high intricacy, high modularity, low phenotypic variance, low genotypic variance, low heritability, universality across cultures and universality across individuals (Andrews et al. 2002; Thornhill 2003; Miller

2000a). All these characteristics need not be necessarily present in all adaptations, but the more we have, the more confident we are that it is not an unselected by-product. Also a cross-disciplinary network of evidence sources needs to be put together to evaluate the validity of each proposed psychological adaptation. The more that different sources of evidence — such as theoretical, psychological, cross-cultural, from hunter-gatherers societies, phylogenetic, medical, physiological and genetic — converge to a particular design of an adaptation the more confident we can be about it (Schmitt and Pilcher 2004).

Aesthetics co-optation and exploitation by artists

It is probable that artistic expression, no matter what its initial sources may have been — mother-infant interaction (Dissanayake 2010), mate choice (Miller 2001) or kinship and tribalism (Coe 2003) — began by exploiting pre-existing aesthetic cognitive biases in various forms and combinations, co-opting its effects to catch the viewer's attention. Co-optation passively occurs when, because of similarity, an input of a different domain is processed in the same manner as the original input of an adaptation, usurping its output effects, and sometimes even super-stimulating it. Given enough time and selective pressure, generations later this adaptation could become phylogenetically exadapted for a different domain, which creates a new adaptation (Andrews et al. 2002).

A proximal example of this kind of process is the aesthetic appreciation of animal and human bodily forms or faces that is evoked by the shapes of clouds. Clouds are just steam blowing in the air, they do not carry any representational aspect, but even so we still sometimes can identify and enjoy animal shapes and human faces and bodies, because of the input similarities to those for which these aesthetic mechanisms were co-opted. Eibl-Eibesfeldt (1989a) has also pointed this out: 'Knowledge determines or biases our perception. Thus, we see figures and profiles in clouds. This knowledge is based, in part, on individual experience, but in part also by prior knowledge founded on phylogenetic adaptations' (Eibl-Eibesfeldt 1989a: 665).

The aesthetic appreciation of human bodily form can also be passively exploited by landscape contour. There are some hill forms that can be seen as a sleeping giant and there are many examples of human faces being perceived in natural rock formations and mountain shapes, like in the Sleeping Giant State Park of Connecticut, Sleeping Giant Mountain of Montana, Sleeping Giant (Nounou Mountain) in Hawaii, U.S.A.; the Thunder Bay's Sleeping Giant, Ontario, Canada, or the Gigante Deitado from Campina Grande, Paraná State and the Gigante Adormecido from Guanabara Bay, Rio de Janeiro State, Brazil (see Helvenston and Hodgson 2010 for more detailed discussion of this phenomenon). This 'preference' for human faces is also exploited by automotive stylists, corporate executives and journalists who appear cognisant of the face-like

properties of the fronts of cars, because the contours of fenders and headlights of numerous cars since the late 1960s have exhibited illusory facial expressions, notably aggressive frowning. The motivation for providing this form of aggressive appearance in automotive styling is consistent with the application of 'muscular' fender lines and large wheels (Coss 1967; Cook 1997).

The human mind has many perceptual biases in which minimal similarity of inputs is enough to easily trigger the pre-existing mechanism. When stimulated, they focus attention, organise perception and memory, and rescue specialised knowledge leading to inferences, judgments and choices appropriate to the original domain. Even newborn babies spend more time looking at a 'T' shape than at an inverted 'T' shape, because of its similarities to the position of the eyes in relation to the nose and mouth in the human face (Farroni et al. 2005). And also three-month-old children gaze longer at attractive faces than at unattractive ones (Langlois et al. 1990).

The cognitive mechanisms that underlie the appreciation of standard forms and order in a given visual situation generally respond to simple aspects of the situation, which has the effect of reducing complexity. The aesthetics of lines, circles, triangles and squares, which allows simple figures offering reduced complexity to attain certain effects give us the simple enjoyment of attractive lines and forms. Organisation and regularisation are signs of intentional control over unpredictable nature (Volland et al. 2003).

The neurological evidence points in the same direction, both on the co-optation aspect of perceptual domain and the aesthetical domain. Grill-Spector et al. (2001) found that the lateral occipital complex in humans and monkeys responds the same way to objects whether real, photographs, or in the form of line drawings. Brown et al. (in prep.), after the most comprehensive meta-analysis of 120 neuroimaging studies of positive aesthetic appraisal across four sensory modalities, found that the most congruent area of activation across all four modalities is the anterior insula, an area typically associated with visceral perception, especially of negative valence (disgust, pain etc.). They also conclude that the aesthetic system evolved first for the appraisal of objects, such as food or sex related, and was later co-opted in humans for the experience of artworks.

The co-optation of the effects of various aesthetics in psychological mechanisms specialised in different non-artistic aspects of our ancestral daily lives, which are exploited by visual arts, can explain the cross-cultural prevalence of representational art, from rock art and tribal art to occidental art (Adam 1963; Eibl-Eibesfeldt 1989a). Aristotle perceived this process because he regarded human interest in representation as an innate tendency. He argued that all kinds of art are imitations of forms of nature. And because for Plato the physical world was already an imitation of the eternal forms, he regarded art as merely imitation of an imitation, since

it represents the natural world in painting, sculpture, singing, acting, prose or poetry (Dutton 2009a).

Exploitation in rock art

Rock art, as painted or engraved images created by ancient humans on natural rock landscapes, is found in most habitable regions worldwide with landscapes containing some natural rock surfaces. Since it is the most visible and symbolic aspect of the archaeological records, its investigation concerning technical and interpretive world variation has experienced a revolution in the last decades and continues to advance rapidly (Whitley 2001). However, as Heyd and Clegg (2004) point out, 'despite the visual attractiveness and strong emotional associations of most rock art, interested scholars, many of them archaeologists and anthropologists, seldom venture to directly discuss it from the aesthetic point of view' (Heyd and Clegg 2004: 1). And Morris stated that 'the challenge we face when evaluating these astonishing [rock art] works is not merely anthropological, it is also a matter of aesthetics' (Morris 1998: viii). Rock art aesthetics means the study, in a general way, of our sensations of anthropogenic marks on rock when those sensations are of interest for and in themselves (Heyd and Clegg 2004).

To analyse rock art literature, we can consider that human beings have a stable intellectual, imaginative, emotional, and aesthetic nature that is universal across epochs and cultures. As Heyd and Clegg (2004) have argued,

if an object from some other society exhibits features we find aesthetically salient then it is at least imaginable that it may have appeared aesthetically salient to some people from that other society. Moreover, if some of the objects under study seem to require an appreciation of aesthetic values in the process of their creation, there is further reason to suppose that some individuals in other societies may have some perspectives analogous to those we call aesthetic (Heyd and Clegg 2004: 5).

Being aware of the nature of our common human condition, we can compile illustrative examples of the most recurrent pictorial motifs of rock art around the world. It is already known that figurative rock art occurs widely, that most sites have not been credibly dated yet, and that in most cases it is impossible to know which exact species has been depicted. Our intention here is to draw attention to the universal prevalence of a specific set of general motifs, such as human-like figures or animal-like figures. Neither the exact species, nor the accuracy of identification, nor the precise dates matter, because these examples are still relevant for providing insight into which pre-artistic aesthetic bias has been co-opted for rock art.

In Europe, Sauvet and Włodarczyk (2008) compiled fourteen figurative motifs from European Palaeolithic cave art — 'horse, bison, ibex, mammoth, aurochs, hind, stag', anthropomorph, 'reindeer, bear, lion, fish, rhinoceros' and 'various/rare'. In Norway, Tansem

and Johansen (2008) have found motifs of humans and animals (mostly 'reindeer', but also 'elk, bears, rabbits, wolves/dogs, foxes, birds, fish and whales') sometimes interacting in large 'scenes' of different kinds of 'activities', such as 'hunting, gathering, fishing, rituals, and dance'; and also motifs of 'boats, fences, geometrical patterns, snow shoe prints and footprints'. In Italy, Anati (2009) found motifs of prey animals, mostly 'deer' and 'cattle pulling ploughs and carts', 'human' figures, geometric designs and 'tools/weapons'. In Spain, Lasheras (2009) has shown motifs of animals, mostly 'deer' ('stags and hinds'), but also 'bison, horses, bulls (aurochs) goats', human faces, hands and geometric designs.

In non-European continents, Campbell and Robbins (2009) found in Botswana, Africa, motifs of wild animals ('giraffe, eland, rhino, zebra, cattle, elephant, antelope, goats and snakes'), geometric designs, 'human' figures and a few positive handprints. In China, Taçon et al. (2010) have found motifs of animals ('stag, deer, bison, goat, horse, bull, bear, cow, donkey and tapir'), geometric designs (rectilinear and curvilinear), 'human' figures and objects ('tools/weapons'). Monzon (1980) and Pessis and Guidon (2007) have shown from Brazil motifs of animals ('deer, bird, ema'), anthropomorphous figures, 'plants', handprints and feet, 'social scenarios' and geometric figures. In the U.S.A., Malotki and Weaver (2001) have found motifs of anthropomorphs, zoomorphs, 'phantasmorphs', phytomorphs, 'manipulable objects', hand and footprints and geometrical designs (rectilinear and curvilinear). And finally, McDonald (2005) has found from Australia, motifs of archaic faces and anthropomorphous figures, animals (birds and other terrestrial animals), and geometric designs (circles, arcs and dots).

Iconographic motifs universally found in rock art can indicate which pre-artistic aesthetic psychological adaptations have been co-opted to catch the viewer's attention. Arguably, it is possible to identify the co-opting of aesthetic appreciation related to at least four pre-existing aesthetic adaptations of those listed by Thornhill (2003): (1) nonhuman animals, (2) human body form, (3) apparent social scenarios, and (4) skilfulness. The representation in rock art of a variety of animals, purportedly mostly prey, humans figures, and humans purportedly interacting in social situations presents the link between the pre-existing aesthetic mechanisms and the co-opted rock art aesthetics. Even the non-figurative geometric designs, besides the bias for skilfulness, can have co-opted basic perceptual aesthetic bias proposed by Eibl-Eibesfeldt (1989a) and Ramachandran and Hirstein (1999), and began as doodles as proposed by Watson (2008).

We are aware of all the taphonomic concerns of representativeness, that it is difficult to know how much of the rock art has been lost and the rock art found today may not represent the totality of motifs used then, but given the similarities between themes

and motifs of pre-Historic rock art and tribal art (Adam 1963) we can be more confident about the validity of this conclusion. And we are also aware of the fact that our compilation is not an extensive review. It is difficult, however, to find cross-cultural comparative reviews of rock art motifs, but even this worldwide compilation of examples on motif findings already gives a very clear vision of its recurrent themes. Many more similarities between non-artistic aesthetics and rock art could be found in future cross-cultural comparative studies of all types of rock art. For us to describe the universal psychology of rock art aesthetics appreciation it would be better to focus on its universal or 'transcendental' pictorial and iconographic quality worldwide. And to do so a standardised nomenclature of motif iconography valid for any style, regardless of its temporal or cultural affiliation, should be developed and adopted to facilitate all the comparative work (Malotki and Weaver 2001).

Up to this point we have presented the plausible origins of our aesthetic cognition involved in the visual arts, focusing on rock art co-opting existing cognitive mechanisms included in the evolutionary aesthetics list. However, two distinct positions emerge from an ancient or a recent focus on this aesthetic cognition. Some authors such as Pinker (2002) argue that this co-opting process is a recent one, so that the aesthetic cognition involved in visual arts is essentially the same as pre-existing non-artistic aesthetics, and visual art would thus be a by-product. The other position, with which we agree, argues that we have art-specific psychological dispositions and capacities to produce visual art and self-ornamentation (Coe 2003; Dissanayake 1988, 1992, 2000a; Dutton 2009a; Miller 2001). In the case of rock art, besides often being very ancient, we think that the co-evolutionary process of sexual selection could have specialised and differentiated some aspects of pre-existing aesthetic cognition in new ways, sometimes in an exaggerated form (Enquist and Arak 1993).

Art fits many criteria for recognising adaptations: It is very old and ubiquitous across human groups, cultures, and history. Art-making and art-viewing are pleasurable for most people. Artistic production entails costs in time, energy, effort and skill. Humans are much better at producing and judging art than any artificial intelligence program or any other primate. Art is relatively fun and easy to learn from an early age, compared to evolutionarily novel skills. Also there is independent evolution of art-like abilities in other species (Dissanayake 2000a; Dutton 2009a; Miller 2001).

Rock art as animal communication

Since it is relatively easy to exapt pre-existing aesthetics to different domains, artists from most historical periods try either consciously or unconsciously to amplify the essence of something in order to stimulate the original aesthetic bias more intensely.

For Ramachandran and Hirstein (1999) the purpose of art is to enhance, transcend or even distort reality, and for Dissanayake (2010) the essence of art is making the ordinary extraordinary and special. But why? The most obvious answer is that it is because of the inherent pleasure of leaving marks and the aim of communicating something in a better way.

A comparison with children's drawings makes this clear. We know of the so-called scribbling phase, which evidently demonstrates nothing but the pleasure of producing something that leaves marks and traces. Kellogg (1970) found regularities that compounded a repertoire of about twelve prototypes of scribbling patterns in children aged from one to three years. Adam (1963) pointed out that in common with primitive artists, children have considerable powers of accurate observation, especially for figurative representations.

They reject everything that is not entirely characteristic, and they often bring out the essential features with surprising clarity. They completely disregard perspective, and observe lines then surfaces. (...) The primitive art which is purely decorative, however, has no parallel in children's art. The young European child never occupies himself with decorative art unless he has been taught to do so by adults (Adam 1963: 75).

Both pleasure and the urge to communicate something are valid answers, but mostly in the proximate sense. For a good model of the evolution of the psychology of arts, we have to look at the evolution of animal communication. Since rock art is human communication and humans are animals, approaching rock art through the framework of the evolution of animal signalling can bring us new insights into rock art aesthetics. Researchers have stressed that the theory of communication borrowed from linguistics has not been very successful in promoting advances in the animal communication literature, and the focus is now changing from informing others to influencing others (Rendall et al. 2009).

The current model of animal communication considers that senders and receivers are under different selection pressures, because selection favours senders whose signals affect the behaviour of receivers to the sender's advantage, and selection favours receivers that are capable of extracting useful information for their own benefit from the sender's signal. Both the manipulation and the informational extraction will feed back into each other, driving a co-evolutionary dynamic that will end either (a) with the disappearance of the signal, due to receivers resisting being manipulated by the sender faking its signal, or (b) with its stabilisation and diversification — with mutual benefits for both sides — into a signal whose design features will reflect this 'arms race' between senders and receivers (Font and Carazo 2010). A computational model of this co-evolutionary dynamic of signalling evolution can be found in Werner and Todd (1997).

Signal evolution and signal design cannot be

understood without acknowledging both strategies, on the one hand the manipulation by the senders of the receivers' bias through perceptual or aesthetic exploitation and on the other hand extraction of useful information about senders' condition for the receivers (Font and Carazo 2010). In the case of rock art, besides often being very ancient, we think that the co-evolutionary process of sexual selection could have specialised and differentiated some aspects of pre-existing aesthetic cognition in new ways, sometimes in an exaggerated form as in other animal signalling evolution (Enquist and Arak 1993).

Sexual selection

Sexual selection is very frequently misinterpreted as sexual motivation, as if sexual selection necessarily always implied sexual motivation and sexual content. However, the product does not necessarily have to exactly mirror the process that has created it, which means that there is no reason for our adaptations to include instructions for how they were selected. Thus, a sexually selected instinct for making aesthetically pleasing ornamentation need not have any association with a desire to copulate, even at an 'unconscious' or 'subconscious' level (Miller 2001).

No introspection can tell us the distal 'why?' behind our liking of sweet food: we like it because it tastes good. Without an evolutionary analysis we cannot get away from this circular thinking. As Dutton (2009a) says '... soul-searching and self-analysis can never by themselves tell you why you enjoy sweet and fat. Evolution, thankfully, gave us capacities and yearning to help us survive and reproduce in the ancestral world — but an explanation from evolution of why we have them was never part of the deal' (Dutton 2009a: 87). Therefore, we need to be careful not to confuse the adaptive evolutionary function of art with the proximate individual motivations for producing art, such as making money, being famous, inspiring religious devotion or challenging patriarchy (Miller 2001).

Sexual selection was proposed by Darwin (1871) and refers to two social processes: intra-sexual selection and intersexual selection. Intra-sexual selection includes male-male competition and female-female competition. The former is more common among mammals. This social process often led to the evolution of traits like weapons through a co-evolutionary arms race. Intersexual selection includes females choosing males and males choosing females, the former being more common. This social process often led to the evolution of ornaments, which can be present on the body or in behaviour and can use visual, acoustic or scent channels (Andersson 1994; Cronin 1991; Ridley 1993).

One evolutionary explanation for the adaptive value of the artistic co-opting of the pre-existing aesthetical biases invokes sexual selection, since it has also been applied to explain non-artistic aesthetic

appreciation (Grammer et al. 2003; Skamel 2003). And by intersexual selection we mean the distal co-evolutionary population level process in which many generations of ancestral males and females interacted entertaining, choosing, surprising, charming and refusing each other, based in part on their aesthetic appeal to each other (Andersson 1994; Grammer et al. 2003). We are not arguing about the proximal motivations such as religious interest, delight in creating figures, substance-induced inspiration, nor other historical explanations such as cultural tradition. This does not mean that proximal and cultural explanations of art aesthetics are not possible, only that at the same time these are different types of explanations, as important as the others, and they need to be investigated.

In the framework of sexual selection, ornaments and displays are considered through the lens of costly signalling theory, which is related to the handicap principle (Zahavi and Zahavi 1997). The idea is that individuals often engage in behaviours that are costly (i.e. involve significant amounts of economic resources, energy, risk or time) as a way of signalling to others useful information about themselves (Bird and Smith 2005; MacAndrew 2002), such as advertising an individual's ability to garner scarce resources and possibly signalling the possession of desirable traits that could be passed on to offspring (Grafen 1990; Miller 2000b; Zahavi 1975). This theory was developed in the field of behavioural ecology and has gained much empirical support in studies of both animal signalling and anthropology (Gurven et al. 2000; Lotem et al. 2002; Smith and Bird 2000; Sosis 2000), and is beginning to influence thinking in psychology (Griskevicius et al. 2007; Miller 2000b; Skamel 2003).

Our appeal to sexual selection is based on a comparative approach. Studies on the aesthetic qualities of animal ornamentation — no matter if it is on their body, such as feather coloration, their phenotype, or a construction done by them, such as the bower of bowerbirds, which is their extended phenotype (Dawkins 1982) — have shown that characteristics that demand much energy, time, capacity or re-sources and are very difficult to be copied by less fit individuals can be seen as fitness indicators. Given the adaptive convergence of many aesthetic ornaments (phenotype and extended phenotype) in different animal species, given animals' displays that are aesthetically pleasing, complex, costly, pompous, big and difficult to copy, and given the relation of ornaments to female evaluation during courtship, it is far more probable and testable that human ornaments are also the product of sexual selection (Andersson 1994; Dutton 2009a; Grammer et al. 2003; Miller 2001; Skamel 2003).

Eibl-Eibesfeldt (1989a) mentioned that aesthetic display plays a major role in courtship and in maintaining sexual relationships. Individual style serves to enhance a positive self-image and suggests that a person is industrious, making him or her a valuable

partner. 'Asked why so much effort went into clothing and objects, the !Kung replied that they did this to show they are "one who knows things and does things" and to be more appealing to members of the opposite sex' (Eibl-Eibesfeldt 1989a: 686).

The classic example of a costly signal is the peacock's tail, whereby the quality of the tail — its size, colour, luminosity and symmetry — serves as an honest signal of the quality of the peacock's genes to potential mates. A high-quality tail is costly to have because it takes much metabolic energy and resources to grow and maintain such a resplendent ornament, which is useless and even detrimental in other aspects of a peacock's life; a high-quality tail is an honest signal of good genes because only those peacocks who are in good health and who have the traits required to survive and acquire abundant supplies of food can afford to waste their energy and resources to grow and maintain this showy and nutritionally costly ornament (Loyau et al. 2005; Møller and Petrie 2002). It is important to understand that for the female peacock, the beauty of the peacock's tail signals attractiveness, not direct viability or genotypic quality: she does not have to know the distal logic of why it is attractive for it to work. Similarly we do not intuitively eat sugar and fat because of its distal evolutionary effects; peahens, humans and all other animals behave because of proximate motivations (Cronin 1991; Ridley 1993).

For a behaviour to qualify as a costly signal, it must meet four criteria (Smith and Bird 2000). First, it must be costly to the signaller in terms of economic resources, time, energy, risk or some other significant domain, whereby the costlier the behaviour the more likely it is to be an honest indicator. Second, it must be easily observable by most people. Third, the display must in some situations for most people ultimately increase the odds that the signaller will gain some fitness advantage through the display, such as increased ability to attract desirable mates. Finally, the signal must be an indicator to potential mates of some important trait or characteristic, genetic and/or non-genetic ones such as access to resources, pro-social orientation, courage, health or intelligence (Zahavi and Zahavi 1997). So our sense of beauty was shaped by evolution to embody a tacit awareness of what is difficult versus easy, rare versus common, costly versus cheap, skilful versus slovenly, and fit versus unfit (Miller 2001).

Arguably, rock art seems to meet all four criteria: (a) it is costly, because you need to spend time learning skills, finding, preparing the material and executing; (b) it is observable, because in the majority of the rock art sites, all your group were able to see the pictures; (c) it could have led to an increase in prestige, if we assume that the painters had a better chance of reaching a high social status due to our common human condition; and (d) it is an important signal of both direct benefits (non-genetic characteristics), such as access to resources made from rare or expensive materials (pigment composition)

and emotional commitment to the context in which art is inserted, and indirect benefits (genetic ones acquired by the offspring) because painting large long-lasting and difficult images or small detailed skilful figures in difficult places requires high ability associated with hand-eye co-ordination, learning faculties, memory, a high creativity level and skilfulness.

Each of these criteria should be empirically tested in future studies. The hypothesis that a behavioural trait has evolved through sexual selection as a fitness indicator leads to eminently testable predictions. Future studies should look for correlations between sexual selection and aesthetics based on three issues. The first is the variation in the design details of artworks produced by representative samples of present people and pre-Historic ones. The variation in the trait should be perceivable, directly or indirectly, consciously or unconsciously, by the opposite sex, in a way that could potentially influence their behaviour, including mate choice (Miller 2001).

The second issue is the variation in the underlying fitness components (e.g. intelligence, personality, health) of those same people. Some studies can evaluate social attribution based on a trait value. The hypothesis is that mate choice systems should have evolved to make the appropriate social attributions on the basis of observed trait values. In the visual arts, this implies that artworks should provoke attributions about the artist's intelligence, creativity and character in opposite-sex observers. In cognitive neuroscience terms, aesthetic judgment tasks given these social conditions should activate cortical areas known to be involved in social attribution (Miller 2001).

The third issue is to evaluate the variation in the beauty ratings assigned to those artworks by other people — preferably young, single, opposite-sex heterosexual people in the same mating market. The 'cost' of this artwork can be an indication of a trait that incurs a significant cost to produce, as measured in energy, time, risk or nutritional resources. These traits also function as good-genes indicators, and should be especially favoured by females during the ovulatory phase of the menstrual cycle, and less favoured at other times. Applied to the visual arts, this prediction implies that women should become more aesthetically discerning during ovulation, more inclined to view art-works as expressions of male talent, and perhaps more inclined to view art ability as genetically heritable (Miller 2001).

It is important to mention that — from the agricultural revolution about ten thousand years ago until now — we humans do not have exactly the same way of life as our ancestors. We expect to find many maladapted behaviours and by-products of exapted learning mechanisms. Our reasoning is applied mainly to our ancestral environment, with selection pressures acting on many generations of humans living the hunter-gatherer way of life, when there were no art markets or money, just rituals, gifts, donation and exchange.

However, this sexual selection explanation would also work if art were a very recent behaviour such as the use of cars to display money, power and social status, but we would not expect to find specific adaptations in this case because their use is very recent. Since we are using a distal theory it is difficult to explain very specific aspects of rock art, such as body postures of the figures, colours preferred, styles, symbolic meanings, religious aspects and so on. These are mostly explained by cultural and proximate theories, and that is why theories of all types are needed. But still, even though it is difficult, some evolutionary aspects have been pointed out regarding figures' body posture and implied motion (Watson 2010) and regarding cross-cultural preference for the ochre red colour (Power 1999).

In the same way, we are not assuming that sexual selection is the only adaptive value for rock art, but one of the possible ones. We are also not assuming that rock art was the only ornament or that only those involved with rock art were able to pass on their genes, but that rock art, among other evolutionary functions, could function as an ornament to impress the opposite sex as possibly did storytelling, music, dance, humour, sports, fight, hunting, gathering and entertaining children.

Aesthetic displays stimulate the psychological biases (cognitive mechanisms) of receivers by attracting attention, provoking admiration, excitement and increasing willingness to mate. So they might have evolved by sexual selection because, on the one hand, they might have had adaptive advantages for the producers by over-stimulating many aesthetic biases in the receivers – by charming them, and inducing a positive perception of the person as well as a perception of higher social status. And, on the other hand, receivers might have had adaptive advantages by observing fitness cues, both genetic and non-genetic. In this co-evolutionary arms race, both image-makers and perceivers benefited (Voland 2003), as in the model of animal communication discussed above.

Eibl-Eibesfeldt (1989a) makes allusion to this co-evolutionary process stating that '[p]erceptual biases specify aesthetic perception. Art exploits these biases either in a playful fashion ("art for art's sake") or uses aesthetic perception to bind attention in order to effectively convey messages, mostly with normative ethical content' (Eibl-Eibesfeldt 1989a: 673). 'The observer's interest and urge to comprehend the message and, so to speak, discover the super signs plays an important role in this process. The positive aesthetic experience of discovery becomes associated with the message being conveyed' (Eibl-Eibesfeldt 1989a: 669).

It is possible to have some hints about the existence of this co-evolution between art producers and receivers by analysing the design features of both art and rock art images, and its aesthetic cognition in regard to the different selective pressure of communication:

benefiting manipulation on the production side, and extracting information on the perceivers' side. On the manipulation side, interestingly and almost independently, Eibl-Eibesfeldt (1989a), Ramachandran and Hirstein (1999) and Dissanayake (2010) came up with a couple of very similar strategic techniques or operations used by artists either consciously or unconsciously to 'capture and to hold attention and to convey sensations of pleasure, interest, arousal, or beauty, associating these feeling with other messages' (Eibl-Eibesfeldt 1989a: 701), to 'optimally titillate the visual areas of the brain' (Ramachandran and Hirstein 1999: 15), and to make ordinary reality extra-ordinary (Dissanayake 2010).

Eibl-Eibesfeldt (1989a) analysed tribal and traditional folk art including paintings, sculpture, music, dance and literature and presented six manipulative operations: (1) creating harmony by emphasising symmetry; (2) creating order by emphasising regularity; (3) creating tension and tension resolution by violating and fulfilling expectations; (4) creating super signs or super stimuli by exaggerating the specific aspects towards those we are perceptually biased to; (5) the joy of recognition by stressing archetypical aspects of things and animals including people; and (6) the joy of re-recognition via the 'Aha' effect by simplification and schematisation offering perceptual, cognitive an aesthetic problems to be solved.

Ramachandran and Hirstein (1999), analysing Eastern and Western classical and folk paintings, images and sculptures, presented their eight laws of artistic experience, which are basically how artists attain aesthetic effects: (1) creating peak shift, accentuations of the definitive traits of something creating a supernormal stimulus, a caricature; (2) reinforcing perceptual grouping and binding during recognition of objects and the 'Aha' effect; (3) isolating a single dimension of a work to allow one to direct attention more effectively and to easily notice the enhancements introduced; (4) creating contrast to focus attention; (5) enable problem solving by letting important aspects hidden or implied to be figured out; (6) avoiding or creating ambiguous images seen from unique view points; (7) creating visual metaphor by accentuating hidden similarities between superficial entities; (8) creating symmetry.

Dissanayake (2010), based on animal ritualisation processes, presented five operations of artification: (1) formalisation, altering form by shaping, composing, patterning, organising, schematising or simplifying; (2) repetition; (3) exaggeration; (4) elaboration; and (5) manipulation of expectation. All these nineteen operations, for the first time put together here, are very similar and complementary in different ways. Rock art studies in the future could focus on identifying each different manipulative operation from this list. Also the work of Palmer et al. (2007), identifying the aesthetic bias related to framed two-dimensional visual media, such as the centre bias and the inwards bias,



Figure 1. An illustrative example of a twisted-horn animal in a Brazilian rock art site compared with a real animal looking sideways. The rock art photograph was taken by one of the authors, JHBPF, the Toca do Boqueirão site in Serra da Capivara Park, São Raimundo Nonato, Piauí, and the animal photograph was taken by Brazilian photographer Ana Irene Mendes. This shows that the manipulative technique of using the canonical orientations by component, as on the twisted horns, is present not only in Europe (Cheyne et al. 2009) or in Africa (Campbell and Robbins 2009), but in South America as well.

should be investigated in presumed scene depictions in rock art.

Mostly independent of all of these authors Cheyne (1993), speculating on the psychology of Palaeolithic graphics, presented five operations used by pre-Historic artists to emphasise distinctive features for better identification of the subject matter of the images: (1) use of occluding contours, simply drawing the silhouette of the figure, especially the dorsal contour, in profile; (2) use of canonical orientations by component, independently depicting each part of the animal from its best perspective, combining the profile presentation of the major occluding bounds of the torso and the head with 3/4 perspective and dorsal/ventral presentation of horns, antlers and hooves, giving the impression that these features are 'twisted'. Actually, Campbell and Robbins (2009) also mentioned that for an African rock art region animals are depicted in silhouette with heads in twisted perspective with two or four legs, two horns and two ears. (3) Change of scale by component, e.g. big body size relative to head size; (4) exaggeration of distinctive features, such as horns, antlers, and the distinctive shape of the cervico-dorsal lines, caricaturising; (5) isolation of distinctive features, drawing only the very typical parts that stand for the whole.

Cheyne et al. (2009) then showed that it is indeed possible to identify the use of a combination of the aesthetic manipulative operations in figurative depictions of large ungulates from the Upper Palaeolithic. They compared measures of parts and proportions of the body between photographs of figurative graphic images of 'horses' and 'bison' with their real living counterparts. They provided quantitative evidence for the hypothesis that certain rock art graphic distortions are neither errors nor idiosyncratic variations, but systematic deviations from veridicality in the form

of caricatures consistent with cognitive principles of graded typicality and contrast in categorisation. They found for the global differences that the most distinctive features of the bison from the horse, the fore-body, is exaggerated in rock art relative to photographs, and the most distinctive feature of the horse from the bison, the hind-body, is exaggerated in rock art relative to photographs. And they found many other strategic distortions on local-feature analyses, such as that the horns of bison in rock art are exaggerated by a factor of two, relative to real bison.

Interestingly, Adam (1963) touched upon the same conclusion when saying that

... the artist's vision and basic tendency are, or were naturalistic. This is modified by an emphasis, or exaggeration, of those details which are particularly characteristic or in which the artist is interested. If we recognise their fundamentally naturalistic — sometimes almost caricaturistic — attitude, we must consider it in our critical appreciation of the work, and, in our judgment of value ... (Adam 1963: 45).

And Gombrich has presented many ways in which arts delude our senses, including the importance of caricature (Gombrich 1962).

The most relevant work on rock art for understanding this co-evolutionary process between image producers and perceivers was done for Villeneuve's master thesis in 2008. By analysing the image's characteristic and the visibility conditions in caves in France, she could identify aspects related from the manipulative and the information extraction roles involved in rock art communication. At the manipulative side, for example, she identified the technique known as anamorphosis, which is highly advanced and consists of proportions depicted in a distorted manner at close range, but seen as normal from specific points on the ground, suggesting that the artist was considering his audience. At the receivers' side of this co-evolution, she showed that the images painted with larger sizes, higher quality and more use of red pigments and polychrome images tend to occur in places where large numbers of people would have been able to see them, while poorer-quality images were more likely to be in smaller places. Perceivers could have inferred level of skill and availability of free time and different coloured pigments from these costly signals (Villeneuve 2008).

Conclusion

We have made some suggestions as to how rock art aesthetics can be investigated from a psychological evolutionary perspective. Seeking to open a genuine opportunity for dialogue between biology and philosophy, psychology and archaeology, we have clarified the role of evolutionary explanations of human psychology by resolving misinterpretations about evolution, natural selection, adaptations, proximate and distal analysis, and sexual selection. We have tried to show that proximate, cultural, and evolutionary explanations of art aesthetics all have to be investigated,

that coexistence is possible, and that all types have much to gain from each other.

A testable theoretical possibility about the evolution of our aesthetic cognition involved in visual arts, focusing on rock art, was presented. We connected rock art aesthetics experience to the co-opting of some specifiable aspects of human nature according to evolutionary aesthetics by compiling the iconographic motifs of rock art cross-culturally, showing examples from Europe, South and North America, Africa, Asia and Oceania, in relation to pre-existing aesthetic biases for nonhuman zoomorphs, anthropomorphs, purported social scenarios and skilfulness. Our examples do not constitute a comprehensive review of the literature on rock art iconography, nor are they meant to; rather, they are intended to offer a basic cross-cultural overview to indicate which set of pre-artistic aesthetic psychological adaptations has been frequently co-opted to catch the viewer's attention since the origins of visual art.

The possibility that the aesthetics involved in art appreciation have originated from our pre-existing aesthetic is a common root for both the adaptive and exaptive positions. Acknowledging animal signalling and the many examples of animals' ornamentation, sexual selection could have acted on rock art appreciation, no matter if it is an ancient predisposition or if it is too recent to be considered an adaptation.

Sexual selection suggests that aesthetic evaluation in rock art is the beginning of a sequence of inferences that reaches all the way from pre-existing aesthetic biases to our social cognition and social attribution, because of fitness indicators. The sexual selection's co-evolutionary nature between image producers and image enjoyers might have intensified the selective pressure upon the psychology underlying rock art aesthetics. And if both sides gain fitness benefits, given enough time, their co-evolution would generate new traits by exaggerating and diversifying ancient traits.

We have proposed that by analysing the design features of both art and rock art images and their aesthetic cognition it is possible to have some hints about the existence of this co-evolution between art producers and receivers in regard to the different selective pressure of communication: benefiting manipulation on the production side, and information extraction on the perceivers' side. We have compiled from different authors numerous manipulative operations used by recent and pre-Historic artists to catch the viewer's attention, give pleasure, induce mood and emotional states that could impress the opposite sex, and ways in which viewers would benefit by costly signals such as larger sizes, higher quality, and more use of red pigments and polychrome images.

And we have suggested ways of testing empirically our theoretical proposal and also we have offered suggestions for future studies deriving from different parts of this article. Quoting Cheyne et al.: 'We may

never fully understand why these images were created but we suggest that we have shown something about why they were created the way they were and something about the nature of minds that created them.' (Cheyne et al. 2009: 107).

Acknowledgments

This research was supported by the Brazilian funding agency CNPq (*Conselho Nacional de Desenvolvimento Científico e Tecnológico*). We authors are grateful to Thomas Heyd and John Clegg for helpful comments on our core idea, to Jerry Hogan for his helpful comments and review of earlier and final versions of this manuscript, and to RAR referees Duncan Caldwell, Ben Watson and an anonymous reviewer for being very supportive, giving many helpful comments and indicating detailed instructions on how to improve this paper. This research was presented in earlier versions as a talk during the Rock Art Aesthetic session at the IFRAO Global Rock Art Congress in São Raimundo Nonato, Piauí State, Brazil.

Marco Antônio Corrêa Varella, Altay Alves Lino de Souza
and José Henrique Benedetti Piccoli Ferreira
Laboratory of Comparative Psychology and Ethology
Department of Experimental Psychology
Institute of Psychology
Universidade de São Paulo
Brazil
E-mails: macvarella@usp.br, altayals@gmail.com,
jh.benedetti@gmail.com

RAR 28-1008

Final MS received 3 December 2010.

COMMENTS

The beauty of rock art aesthetics

By BEN WATSON

A detailed study of the evolution of aesthetic displays in rock art by sexual selection has been lacking, and although the idea is not a new one, Varella and colleagues make an important contribution to existing literature on the evolution of human artistic cognition. I agree with the authors that a focus on recurrent imagery types is the most appropriate means of understanding the underlying psychological bases of rock art aesthetics appreciation. The data presented provides further support for a thesis I have argued at some length: that the exploitation of evolved perceptual biases and universal aesthetic sensibilities is reflected in the most common forms of imagery in hunter-gatherer rock art worldwide (Watson 2009). Abstract-geometric motifs and patterns, anthropomorphs and zoomorphs are all shown to have special roles in visual information processing, and this appears to have strongly influenced

preferences and decisions made in the process of creating rock art throughout time and space. The most commonly recurring forms are in fact precisely those visual stimuli that are particularly powerful triggers of the neural activity underlying aesthetic responses and correspond with prominent areas of the visual brain. The neural mechanisms involved have typically developed during human evolution specifically for the analysis of biologically significant aspects of the visual world. For example, specialised neural structures for the visual processing of human bodies and parts of human bodies such as hands have developed in large part because of their great importance in social life and communication. The human body and its parts are subsequently very effective as visual images and capable of evoking strong aesthetic responses because they activate neural networks specifically attuned to processing them (Watson in prep.). I do not propose, as implied by the authors, that non-figurative geometric designs or a perceptual aesthetic bias for them *began* as doodles (Watson 2008). Rather, I have suggested that aesthetic sensibilities towards basic abstract-geometric forms, mediated by underlying neurophysiology, are reflected in the process of creating doodles, as in other forms of mark-making, and that they may influence the selection of certain forms for depiction.

As intimated by the authors, the idea that certain forms are inherently pleasing goes back at least as far as the ancient Greeks. Modern proponents considering the theory in more detail, such as Gombrich (e.g. 1978, 1979), have suggested that certain motifs correspond with psychological dispositions and that the attraction to certain forms lies in their biological relevance. Recent advances in neuroscience have helped to develop these ideas much further, resulting not only in a means of approaching earlier philosophical theories of aesthetics such as those of Plato and Aristotle (see Paul 1988), but an increasing number of studies revealing important evidence for a neural basis of aesthetic preferences (e.g. Zeki 1999). Today, notions such as a universal concept of beauty or positive aesthetic judgements on art must be based on specific psychological adaptations and neurophysiology. As the authors point out, neuroanatomical correlates of aesthetic preference have been observed in neuroimaging studies, including preferences for 'beautiful' stimuli amongst representational and abstract paintings (Cela-Conde et al. 2004; Jacobson et al. 2006; Vartanian and Goe 2004). For example, in a functional magnetic resonance imaging study, Kawabata and Zeki (2004) used portrait, landscape, still life and abstract composition paintings as stimuli, and found that objects perceived as beautiful produced greater activation in brain structures associated with emotion, such as the orbito-frontal cortex and anterior cingulate cortex. The motor cortex was also found to be active, suggesting that the perception of beautiful and emotionally charged visual stimuli mobilises the motor system to take some form of physical action (Kawabata and

Zeki 2004: 1704). This may relate further to responses afforded by certain formations in graphics indicative of biologically significant stimuli, including instinctual behavioural reactions such as avoidance (see e.g. Watson 2011).

The importance of neuroscientific findings is clear when considered in combination with theories such as sexual selection. The authors are wise not to posit sexual selection as the only motivation for rock art; however, it is important to stress that aesthetic evaluation in rock art does not necessarily relate to fitness indicators and assessing genetic worth. Late Acheulian bifaces have been similarly argued as products of sexual selection on the basis that they are highly symmetrical, often lack use wear and appear to exceed their functional requirements (Kohn and Mithen 1999; Mithen 2003). But as Hodgson (2009a, 2009b) has pointed out, this interpretation is not in total agreement with neuroscientific data, which suggests that rather than being associated with health and genetic quality and thus adaptive fitness, the traits of such tools can be explained simply in terms of exploiting the perceptual sensitivity for symmetrical forms that evolved through natural selection for purposes imperative to human survival, such as discriminating predators and prey from inanimate objects. Preferences for symmetry and other perceptually salient forms including any number of motif types commonly found in rock art may thus appear where a signalling context is not obvious, such as in exploratory behaviour, response to patterns and object recognition (Enquist and Arak 1994). Perceptual biases can therefore account for common characteristics of rock art content without recourse to sexual selection, and need not have become phylogenetically exapted for such a purpose.

An interesting aspect of the theory is the implications sexual selection for artistic display has for understanding the authorship of rock art. Although in most cases it is unclear whether those who produced it were male or female, it has been suggested on the basis of differences in male and female neurology that males (particularly adolescents) are more likely to be responsible, at least for a majority of European Palaeolithic art (Bednarik 1986: 48, 2008a; Guthrie 2005: 327). This might help to explain the recurrence of certain motifs such as depictions of genitalia, nude anthropomorphs and large mammals. A greater degree of male competitiveness might also suggest reason for the prevalence of male rock artists. However, it must also be noted that males are by no means more artistically skilled, and females have participated in artistic endeavours as much as or more than men throughout time. Furthermore, the diversity of rock art imagery does not suggest authorship by adolescent males alone. A weakness thus exists in the comparative approach taken by the authors concerning the notion that it is more common in intersexual selection among mammals for females to choose males on the basis of their artistic ornaments.

These reservations aside, I believe this is an im-

portant paper, particularly in the positioning of evolved psychological biases within a discussion of the evolution of aesthetic displays in rock art by sexual selection. It is particularly valuable in providing further support to existing neuroscientific and evolutionary theories that account for the prevalence of certain forms of rock art imagery. Varella and colleagues are commended for undertaking an ambitious study, and for their success in generating further interdisciplinary dialogue on the topic.

Dr Benjamin Watson
1/83 Maltravers Road
Ivanhoe East, VIC 3079
Australia
E-mail: watson.benjamin@hotmail.com

RAR 28-1009

Art as a tryst

By PATRICIA A. HELVENSTON

'It has been said that art is a tryst, for in the joy of it, maker and beholder meet' (Kojiro Tomito). I chose this quotation to comment upon *Evolutionary aesthetics and sexual selection on the evolution of rock art aesthetics* by Varella, de Souza and Ferreira because the focus of their paper is upon the Darwinian sexual selection of rock art as a communicator of fitness, as well as a communicative signalling device between artist and onlooker. In other words they have chosen to spotlight their discussion on the co-evolutionary adaptiveness of both artistic creation and appreciation for both the maker of 'art' and the audience viewing it.

This paper presents a somewhat 'shotgun' approach to the discussion of these issues with an impressive bibliography and a scattering of briefly considered but numerous lists of aesthetic adaptations (Thornhill 2003: 27), neurological characteristics of artistic expression (Ramachandran and Hirstein 1999), manipulative operations of traditional art (Eibl-Eibesfeldt 1989a) and ritualisation processes (Dissanayake 2010, for example; I think a more in-depth discussion of the work of Ellen Dissanayake [2006, 2008] as it relates to the main theses of this paper would have been more useful). In contrast to the authors, I doubt very much that any special adaptation for rock art has evolved either as a signal of fitness or for the purpose of communication. Rather, a very general adaptation for 'artification' ('making special' according to Dissanayake 1995) seems much more likely to encompass the production and appreciation of rock art. Nevertheless it is gratifying to see such an interesting, multidisciplinary paper published in *RAR* because it continues the policy of fostering vigorous discussions pursued by the current editor who has endeavoured to ground the publication in not only the arts and humanities, but the biological

and social sciences as well.

I will restrict my comments to a brief discussion of the mechanisms of selection which evidence demonstrates are likely to account for the evolution of aesthetic appreciation and 'making special' which characterise all the arts. The authors stress the importance of sexual selection for 'fitness' as one of the crucial adaptations encompassing the production and appreciation of rock art. The theory is that animals have developed highly aesthetic displays which are appreciated by the opposite sex and thus conspecifics with such displays are innately preferred by a process of sexual selection and they thus contribute their genes to the genotype. Certainly a very broad appreciation favouring such displays (the *Art instinct* of Dutton 2009b), as well as an aesthetic appreciation of the natural environment (the Biophilia of Wilson 1984) has a long history of adaptation reaching back into primate evolution.

For example, though they appear to be incapable of producing anything representational, chimpanzees seem to enjoy drawing indiscriminate shapes with some sense of order and will pursue such activities for long periods of time (Morris 1962). Adrian Kortland (1962) described observing a wild chimpanzee come into a clearing and sit staring at a vivid sunset for about 15 minutes. The chimpanzee then left without taking any food that was also present in the area. Sexual selection could have been acting upon a general suite of 'aesthetically special' perceptions and behavioural responses for millions of years prior to the earliest hominins (Dissanayake 1995; Miller 2001).

However, human culture is likely even a more powerful factor in rapidly selecting desirable aesthetic traits, at times with deleterious consequences and could result in a fairly rapid selection for artification. Indeed, domestication is likely the most parsimonious explanation for the fact that natural selection has not weeded out a number of neurodegenerative diseases and brain disorders which may accompany higher cognitive and artistic abilities (Bednarik and Helvenston in press; Helvenston and Bednarik in press; Bednarik 2008b; Nettle and Clegg 2005; Goodwin and Jamison 1990: 332-366).

Chase (2010: 14) provides a multifaceted definition of human culture and based upon an extensive, data-based theory he proposes that humans had a complex culture from the mid-Pleistocene. Following is some of the evidence supporting this idea. Body painting and adornment probably dates to some 300 000 years ago as testified by a large collection of yellow, brown, red and purple ochre found at Terra Amata near Nice, France (Hadingham 1979). Some of the earliest artistic representations include the Tan-Tan figurine, dating to 300 000-500 000 years ago (Bednarik 2003) which demonstrates a possible appreciation for an anthropomorphous-appearing figure. Also, the grooved pebble from Berekhat Ram, dating from before 233 000 years ago, with deliberate incisions to more clearly delineate the head and arms also suggests the

appreciation of a human female-shaped rock, along with intentional attempts to embellish the figure to make it appear more life-like (Goren-Inbar 1986: 11; Marshack 1997)

Subsequently, we have evidence from Blombos cave of shell beads (Henshilwood et al. 2002) and of engraved art works dating from 78 000 years ago (Henshilwood et al. 2004) documenting a culture utilising simple geometric forms (a precursor of symbolic writing systems?). Thus, the material record supports a gradual evolution of 'making special' (in the visual arts particularly) for the past 300–500 000 years. In addition to the forces of biological sexual selection operating on behaviours of personal adornment, human *culture* itself has placed a high value on artification, thus magnifying any strictly biological effect of sexual selection.

For example, developmental systems theory challenges the focus of natural selection on the genes with a model of interacting systems (Oyama 2000; Oyama et al. 2001), emphasising non-genetic inheritance of traits and the cybernetic feedback from organism-environment systems changing over time. In niche construction (Odling-Smee et al. 2003), organisms modify the evolutionary pressures acting on them through culture. Laland et al. (2000, 2010) and Mesoudi et al. (2006) see much of niche construction as guided by socially learned knowledge and cultural inheritance (Silk 2007). Other proposed non-genetic dimensions of evolution are epigenetic, behavioural and symbolic inheritance systems (Jablonka and Lamb 2005).

While sexual selection may have been operating for the earliest hominins, domestication and other models of cultural selection provide a more plausible explanation for the development of a broad adaptation of artification in the evolution of *Homo sapiens* than sexual selection in a strictly Darwinian sense of the term for the past 300–500 000 years. In other words, a dual inheritance model including sexual selection for the great apes and early hominins augmented by cultural selection of artification since archaic *Homo sapiens* seems indicated.

Dr Patricia A. Helvenston
1407 N. Aztec Street
Flagstaff, AZ 86001
U.S.A.
E-mail: Patscholar@aol.com

RAR 28-1010

Sex for its own sake

By LIVIO DOBREZ

Despite art-historical leanings in the direction of a Virgin Birth, somewhere in that space/time perplexedly dismissed by Gombrich (1972: 19) as

'strange beginnings' and effusively embraced by Bataille (1980: 11) as '*le miracle de Lascaux*', art and the aesthetic must have more or less definable origins. Even if you take Darwin's version of evolution as merely the best currently on offer, it is not unreasonable to postulate an evolutionary psychology and in line with that to try to put aesthetics in Darwinian perspective — provided you prudently refrain from Gordian-Knot cutting. Varella et al. do not claim to explain everything, though they run quite a hard line. The first issue must be that available definitions of 'aesthetic' and 'art' are historically recent and hard to set aside for the purpose of a long evolutionary view. Art for its own sake (*'l'art pour l'art'*) was a slogan coined by Théophile Gautier in the mid-1830s and taken up by the Parnassian movement in the 1860s. Its pithiest expression in English was given by Wilde in the notorious preface to *The picture of Dorian Gray* ('all art is quite useless'); its most lucid, by Joyce in the final section of *A portrait of the artist as a young man*, where (aesthetic) stasis is set against (practical) kinesis. In culture-historical terms all this comes out of the emergence of the bourgeoisie with its cult of 'sensibility'. Philosophically, most of it comes out of the Germanic tradition which invented the discipline of aesthetics in the mid-18th century (Hammermeister 2002) and in particular from Kant's 1790 *Critique of judgement* which identifies the aesthetic as 'disinterested' pleasure. Like Darwin in *The origin of species* and *The descent of man*, Varella et al. assume something like this context for their presentation of the subject — though they might have been more wary, like Clegg and Heyd when the latter are quoted as referring to societies with 'perspectives *analogous* to those we call aesthetic' (my italics).

There are people who think that the 'aesthetic attitude' is a myth (Dickie 1969), i.e. that there is no specifically 'aesthetic' attitude — in which case what we term 'aesthetic' would have to be located in the *object* of such an attitude (see Dutton 2009a: 52). But this argument is hard to sustain when, demonstrably, *any* object, including Duchamp's *pisseoir*, is liable to evoke an aesthetic response. Assuming this response is not a myth, we still need to be cautious about calling it a 'pleasure' or, if it comes to that, an 'emotion'. Aesthetic response, as Varella et al. acknowledge, need not be pleasurable. Even if we allow the soft term 'emotion', the question is 'of what kind?'. Ramachandran and Hirstein (1999) stress the visual system's constant connection with the limbic. So far so good, until a leap of logic turns emotion into an *aesthetic* emotion, generated by an apparently Kantian amygdala. I would prefer to speak of an aesthetic 'judgement', but without Kantian baggage. The aesthetic would then be a stance you assume towards the properties (not necessarily simply good or bad) of an object (a person, a flint artefact, a sunset, a picture). These properties would have to be taken as *formal* ones (and here we cannot escape our own historical horizon), with the understanding that formal properties may serve practical and/or symbolic

ends and raise, in the final analysis, issues of truth.

On the question of aesthetic judgement predating art-making, the jury remains out, it being much harder to speculate on the origins of such judgements than on the origins of making a mark (on artefact, body or rock). Perhaps it is too problematical to imagine marks being taken as 'aesthetic' without a prior disposition to the aesthetic. At the same time our evidence for a primordial aesthetic must be based on the presence of artefacts or suggestions of body decoration and the like. So we assume an aesthetic as prior to art on the basis of art (a term, incidentally, eminently applicable to Acheulian hand axes from West Tofts or the finely-worked cupules at Daraki-Chattan). At any rate



Figure 1. Set of apparently arranged cupules on the wall of Daraki-Chattan Cave, central India: an example of possible 'aesthetics' in one of the earliest known palaeoart sites. Photograph by P. Dobrez.

Varella et al. follow this problematical logic, as indeed I would be inclined to do. They open their argument by taking an evolutionary psychology stand on the adaptive value of art and the aesthetic, contra Pinker (2002) who thinks the latter is adaptive but the former not, and pro Dissanayake (1988, 1992, 2000) and Dutton (2009a), who regard both as adaptive. This is of some importance, since without such a stand they could not proceed to an evolutionary aesthetics. Actually the authors gloss over exaptation as a relevant concept in their first paragraph, dodging the Gould vs adaptationist debate, though they clearly identify with the adaptationist agenda. The debate might be stated here as follows: are aesthetic judgement and its material manifestations to be taken as Gould's San Marco dome or merely its spandrels-in-waiting? Following the logic of Elisabeth Lloyd, the second option would make the aesthetic comparable to female orgasm as a by-product of male orgasm. Gould's idea of the role of 'unemployed' characters was put forward in 1979 (with Lewontin), made prominent in 1982 (with Vrba) and given lengthy exposition in *The structure of evolutionary theory* (2002: 1179ff). It is gleefully ridiculed as 'the spandrel's thumb' by the cruel Dennett (1995: 267ff). As far as Varella et al. are concerned, aesthetics has to have the status of employment, i.e. current utility. Leaving aside spandrels and exaptations (concepts with, in my view, highly relevant implications), let us tentatively assume that beautiful hand axes and cupules (well ahead of Chauvet) satisfy enough conditions to be regarded as adaptive, or at least as fair candidates for adaptation.

If that is the case evolutionary aesthetics is up and running and Varella et al. accordingly open their case with it. The concept of beauty, they argue, though not culturally-variable applications of it, is universal. They then move to consideration, in turn, of what I am calling aesthetic judgement and of art-making. Re aesthetic judgement, they establish parameters with Thornhill's ten areas of experience in which aesthetic judgement may be involved. My concern here starts

with the ease with which they immediately add a few more (neoteny, flowers etc.) to the list, showing that it has no particular authority. Not that this observation would worry Thornhill, who casually suggests that the special-purpose nature of adaptations means that there is no discrete psychological operation corresponding to the term 'aesthetic'. This despite his article being about something called the 'aesthetic'. I appreciate the apparent diversity of the aesthetic and hence the attraction of a 'cluster' approach to its analysis (see Dissanayake 1988: Ch. 2). But there has to be some attempt at integration, and Thornhill offers none — other than use of the term 'beauty' (which here means nothing more than having a liking for something) because it is there. It follows from all this that the ten 'domains', each generated by a unique adaptation, have no necessary connection with each other — which leaves me wondering what exactly Thornhill's list is a list of and accordingly what use anyone can make of it. Re art-making, I have no difficulties with the suggested mechanism of co-optation. I see a problem with the predictable (because culture-specific to *us*) conflation of art-making with mimetic representation. Is such representation, as stated, the historical norm? And is it likely that the original marks made by humans were *likenesses* of things? This in spite of Greek concepts of mimesis and the status accorded to mimetic realism, most recently by Gombrich — and for Varella et al. by Dutton (2009a: 55).

The other reservation I have about this otherwise plausible phase of the argument is the model implicit in the language used to describe the genesis of art: 'artists' are said to 'exploit' an existing aesthetic capacity in order to 'catch the attention' of an audience. If we are to distinguish between proximate cultural motivations and evolutionary explanations, our model cannot be the modern one of individual and defined 'artist' keen to attract an art public. Given a few ethnographic parallels, it would make more sense to think of a group activity generating art-making on the basis of existing

capacities and for the adaptively useful outcome of more nuanced social communication. I realise that group selection is, for some, a problematical idea, but it seems to me that in the present discussion it could provide a necessary conceptual bridge between natural selection and culture. The application of the Varella et al. argument to rock art is straightforward. However, the authors continue to promote the mimetic line, in which connection I think it would be possible to make the larger point without prioritising the role of figurative representation. Moreover their appeal to Thornhill's list means that this move can have no more validity than Thornhill's avowedly selective list. In any case, as the authors realise — without acting on it — taphonomic logic makes short work of any notion of 'representative' rock art motifs.

We now come to the last two sections of the argument. Authorities as diverse as peacocks and bower birds on the one hand and neuroscientists and fellow-travellers on the other, tell us that art has to do with over-the-top activity. Dissanayake may be right about making things special and Ramachandran and Hirstein may, in their gloriously cavalier way, be partly right on art as 'enhancing', 'transcending' and 'distorting' (though these three are very different effects, and 'distorting' once more rears the time-we-buried head of Gombrich mimesis). I am not convinced that art, understood in terms of group hunter-gatherer activity focused on place and story and geared to metaphysics rather than 'imitation of nature', is primordially a 'display'. But I see why Varella et al. want to press the case: it leads straight to Darwin's other mode of selection, the sexual, to which Darwin appeals in his consideration (somewhat revised by present-day evolutionists) of that 'peculiar [sic] kind of pleasure' associated with the 'beautiful for beauty's sake' in the *Origin* (1928: 186) and the 'pleasure ... which may fairly be called a sense of the beautiful' in the *Descent* (1952: 301). In each case, of course, the terms are broadly Kantian. Varella et al. have to make Darwin's logical leap here — from mating birds to art — moreover defining art as a form of exaggeration. Darwin made the leap in the *Descent* by pointing out that 'women everywhere deck themselves with ... plumes' (1952: 301) and undoubtedly there is a powerful *prima facie* case here: think aesthetically and you may well think of attractive bodies at the carnival in Rio. On the other hand this logic, if it applies at all to art objects, does so indirectly, though there is no shortage of sex scenes in rock art and in many other representational traditions (Khajuraho, Radha/Krishna miniatures, Ukiyo-e erotica, European nudes from Apollos and Aphrodites to the Italian crucified Christ, from Botticelli, Michelangelo and Titian to Picasso, not to mention the movies). Certainly in the case of artfully presented bodies in Rio sexual selection would seem to be hard at work. But we need an argument rather than intuitive leap here. Varella et al. appeal to 'costly signalling' criteria, most of which, however, do not, in my opinion, readily apply to

rock art. Like Ramachandran and Hirstein the authors suggest possible experiments which, if I understand correctly, would involve, among other things, a group of ovulating Catholics, to test correlations between aesthetic judgements and sexual preferences.

We are back to Joyce's stasis and kinesis and I fear an experiment along these lines would fail the sophistication test. Still, let someone try it. Along the way, past those (supposedly) scientific and (surely) aesthetically painful formulas of manipulating and extracting, not to mention co-evolutionary arms races (a language which tells us more about contemporary cybersociety than either art or sex), there are nineteen art characteristics as set out by Eibl-Eibesfeldt, Ramachandran and Hirstein, and Dissanayake. Many of these, especially those proposed by the first three authors, may be sourced to Gestalt psychology. In all cases, though, the connection with kinetic desire is far from obvious. The thesis may be true, but the argument for it remains problematical. In the event of its being true, where does that leave gay art curators in the world's major galleries?

Dr Livio Dobrez
College of Arts and Social Sciences
Australian National University
Canberra, ACT 0200
Australia
E-mail: livio.dobrez@anu.edu.au

RAR 28-1011

'My glyph is more beautiful than yours' — but does it matter?

By ELLEN DISSANAYAKE

To my knowledge, the article by Varella and colleagues is the first published examination of the evolution of rock art aesthetics from the viewpoint of current evolutionary psychology. As such, it is long overdue. The authors' ideas are admirably well-grounded in recent theory and research in the fast-developing fields of evolutionary psychology in general and evolutionary aesthetics in particular. Readers will find many excellent references for further exploration of the topic.

Discussions about art from any point of view are often confusing and confused, not only because use of the term has been historically ambiguous but because it is not always clear whether one is referring to a behaviour (making), a product (the object or 'work'), or to psychological appreciation ('aesthetic' experience). The authors are aware of this difficulty and say that their primary concern is with aesthetic experience (sometimes also called aesthetic cognition or aesthetic psychology). Art-making behaviour, however, does

become important when the authors advance their sexual selection argument six pages into the article, after they justify using an evolutionary explanation of aesthetics and describe aesthetic psychology in general.

For newcomers to this new field, it should be said that evolutionary aesthetics (EA) (e.g. Thornhill and other articles in Voland and Grammer 2003) has little to do with 'aesthetics' or 'aesthetic experience' as commonly regarded by philosophers of art. Rather, EA takes as its province all sensory/cognitive appreciative experience on a continuum of liking or preference at one end and disliking or avoiding at the other. Something that is greatly liked or preferred (a bright colour or clear sound) has probably had adaptive advantage in our evolutionary history; something that is disgusting or aversive (a dull, dirty colour or muffled sound) was harmful or otherwise disadvantageous. In our pre-Historic past, 'aesthetic' preferences and choices thus guided us to behaviour ('approach' or 'avoidance') that led to greater survival and reproductive success than not having these preferences or choices. In this regard, humans are like other living creatures.

Humans, however, make and regard art. For EA theorists, then, 'aesthetic' appreciation of art works is based on responses to certain of their features that were adaptive in non-art contexts but used by artists (often inadvertently) in their work. For example, we may like glossy surfaces because they unconsciously remind us of the sheen of clear water (Coss 1990) or of glistening nutritious pig fat (O'Hanlon 1989); clear true colours suggest ripe fruit; curved lines are soft and restful while jagged ones are like sharp fangs or thorns; soft, melodious sounds are pleasant because they are non-threatening, and so forth. Our sense of beauty, according to EA, derives from being attracted by those sensory and cognitive features that enhanced fitness in ancestral environments.

There are a few difficulties with this general view of things. Responding with attention and interest to signs of biological importance (whether positive, negative or indifferent) is the first step in our emotional appraisal of anything. Evolutionary aesthetics (like neuroaesthetics) has not found a way to differentiate between objects that are called 'art' and non-art (Brown and Dissanayake 2009). One can certainly look at a known or accepted instance of art and find features in it that might have had biological relevance in the past. But these are not necessarily what make it 'art' in the modern sense. An image of a wounded bison with entrails hanging or a carved vulva immediately and understandably attracts notice: these are of emotional interest. But to be accepted as art, *something more has to be done* than merely display the signal. For example, the work's placement may be important: its contours may be simplified and arranged with regard to its immediate site and larger surroundings (if other images are already present); often parts of the image are omitted or exaggerated; there may be repeated or elaborated components; an

unexpected element (leading to surprise) may be part of the whole conception and effect. That is, choices other than subject matter or sensory stimuli are critical to our modern response to artworks. We respond differently to a colour photograph of a bloody carcass or a *Playboy* centrefold image than we do to Rembrandt's *Flayed Ox* or *Saskia in Bed*.

The authors, and other theorists of evolutionary aesthetics, might reply that they are not concerned here with appreciating Rembrandt's paintings (although their ideas are applied here to Pleistocene paintings and engravings). What muddles the discussion is their use of the word 'art' since they could just as well use words like 'image,' 'glyph' or 'marking', and not introduce an ambiguous and confusing word, art, at all.

Or they could re-conceptualise their theoretical framework. Although this response is not the place to present my own view of rock art aesthetics, I will briefly digress to say that I consider it helpful to situate the making of palaeoart, along with other arts, in a broader, prior category that I call 'artification' (Dissanayake 2007, 2009, 2010/11). Archaeologists frequently assume that the appearance of 'art' provides a window into ancient human minds and social groups, indicating their degree of human intelligence or cultural development. In contrast, I claim that art, considered ethologically as a behaviour of artifying (rather than as artefacts or products of that activity — e.g. engravings or paintings on rocks or walls, shell beads or bone instruments), can be usefully regarded as a biologically distinctive and noteworthy characteristic of humans in itself, not simply as a subset or by-product of their intelligence, symbolising ability or cultural level. That is to say, artification — intentionally making parts of the natural and man-made environment (bodies, surroundings, shelters, clothing, tools, utensils, weapons and other paraphernalia) extraordinary or special by marking, shaping and embellishing them beyond their ordinary functional appearance — is a heretofore undescribed (or overlooked) capacity in the human repertoire. Calling these activities artification (rather than art) avoids connotations of value, beauty, skill or representation inherent in the modern Western concept.

Indeed, with this fundamental theoretical construct, a 'behaviour of artification', one can say that the Pleistocene mark-makers discussed by Varella et al. used the pleasing, striking or 'beautiful' stimuli of EA, sometimes (but not necessarily) symbolically and skilfully, to artify objects, environments, sounds, movements and occasions. In other words, the elements described by EA are not synonyms for 'art' (an abstract, largely useless category in the context of palaeoart) but rather *means to artification* (a broader and definable pan-human capacity or behaviour applicable to the making of 'art' anywhere and by anyone).

In the case of palaeoart, an important evolutionary question is not only 'What makes something art — an item for aesthetic appreciation?' but 'Why did someone

make the effort to carve, peck, hammer or paint a rock surface in the first place?’

To this question, the authors offer the popular evolutionary argument of sexual selection. This explanation does not require that an art-maker consciously think ‘By showing my skill, I will attract mates’. Rather, over evolutionary time, those who displayed their superior and biologically costly artistic abilities tended to attract more fertile and desirable mates so that they and their offspring had better chances of survival and reproduction compared to less gifted conspecifics whose marks were less admirable or nonexistent. (‘Costliness’ refers to the expense of time and physical effort that could otherwise be directed towards other adaptive behaviours like hunting or even resting, as well as the possibility that an absorbed artist might expose himself to dangerous predators or human enemies).

Varella et al. propose that the male ability to *make* rock art images co-evolved with the female ability to *appreciate* their skilful rendering of naturally-appealing features. Both abilities would be inherited by their offspring, who themselves would then become artists or appreciators who used (or appreciated) new and more appealing fitness-indicating features more skilfully, and so on down the heritability chain.

Despite the fact that human males, like males in other species, undeniably use costly signals — including art-making — that might attract interest from females (as well as gain admiration from other adults, leading to a higher social status), I find the sexual selection argument inadequate to account for the evolution of rock art aesthetics. (The authors themselves admit, two pages from the end of their article, that sexual selection is only one possible adaptive value for rock art, but ‘one of the possible ones’).

For one thing, the sexual selection argument is really about beauty (appeal and attractiveness), virtuosity or skill, and originality in any act or feature. Yet not all art is beautiful — it can instil apprehension or even fear and still be effective. Not all art is skilled — in many traditional societies, participation at any level is valued more than skill in drumming, dancing, singing and self-decoration (Chernoff 1979). In Yupik painting, stylised simple representations to accompany a story are valued over aesthetic effect (Himmelheber 1993 [1938]: 11, 28; see also Horton 1965: 39–40; Stott 1975: 38). Not all art is original — in most traditional societies, novelty and originality, values in the modern West, are often discouraged (Aiken and Coe 2004; Coe 2003). What is more, once anything has evolved, it can be used for competitive display. A vulgar example I sometimes use is that of male urination. Schoolboys or drunks may compete as to whose stream goes furthest or highest. Yet no one would say that urination through a penis evolved for the purpose of male display or competition.

The authors’ choice of *representational* rock art images skews their evolutionary scenario to an emphasis on skill (accurate rendering), which then logically leads

to a sexual selection explanation of the evolution and adaptive function of rock art. Let us for heuristic purposes choose as our focus *noniconic* imagery which, after all, occurred on all continents before iconic depictions (see below). Rather than portraying recognisable subject matter, these ‘geometric’ marks or designs arise in part (as they do in children) from natural motoric movements of the hand and arm (Steven Brown, pers. comm. 2010) and their appeal may be traceable to universal neural processing that is based on visual perceptual primitives and satisfying Gestalt-like configurations (Hodgson 2000; Bednarik 2006). Compared to representational imagery, the reason for making such marks is not so easily explained by a costly signalling or sexual selection hypothesis.

Criteria for costliness include observability. In palaeoart, it is not clear how often mark-makers did their lengthy and arduous engraving, pecking, hammering or painting in plain sight of others. We do know that at least some of these marks occur in places difficult of access or visibility. Moreover, it is not certain that rock artists would have necessarily gained renown among their associates. A recent modelling exercise of petroglyph production in the Picacho Mountains of southern Arizona provides data suggesting that over the 3800 year span during which petroglyphs were made (3000 BCE to 800 CE), the number of recorded known and assumed unknown designs amounted to a rounded 4650, yielding one design per year total for the entire Picacho Mountain range (Wallace 2008). If the sample is restricted to Western Archaic petroglyphs over the same period — an estimated 400, all of which are noniconic — then we find ‘an average of one-tenth of a design element pecked per year, or 10 elements pecked per century’ (p. 227); doubling or tripling the figures to account for potential loss through erosion or other taphonomic factors does not appreciably change the results.

Wallace points out that if most of the Picacho glyphs were manufactured in a short period of time, as is suggested by clusters of designs at the largest sites, ‘many hundreds of generations of early hunter-gatherers in the area did not hammer out any designs at all, and petroglyph production can hardly be considered a ritual tradition’ (p. 227). He concludes that (1) only a small number of individuals in any particular pre-Historic society ever made rock imagery; (2) on average, they did not do it very often; (3) individuals from only a few of the many communities in any given region may have been involved in their production; and (4) because making rock imagery was not an everyday occurrence, when it was made, it may have had special significance (p. 228).

Wallace’s paper contains much more information than provided here and deserves to be more widely known. Its recent date and restricted availability explain why it was not known to Varella and his co-authors. Although Wallace’s findings do not address representational images, they do strongly suggest

that a sexual selection hypothesis is irrelevant to the infrequent production of noniconic Archaic imagery in the American Southwest.

This is a serious consideration since it should be remembered that the earliest palaeoart everywhere, spanning scores of millennia, is noniconic. For example, in about 97% of the area of Eurasia, graphic Paleolithic palaeoart — where it occurs — seems almost entirely restricted to geometric or non-iconic marks (Bednarik 1993). The well-known galleries of painted animal masterpieces in some Franco-Cantabrian caves are remarkable but they are hardly representative of the evolution of palaeoart. Even in these caves, the few thousand zoomorphic images are outnumbered several times by noniconic marks (Bednarik 1993). Granting that the authors' hypothesis is restricted to representational images, are we to assume that the much larger number of makers of noniconic marks (and males who did not make marks at all) were doomed for millennia to second-rate mates and fewer, clumsier children?

It should also be pointed out that the field of evolutionary aesthetics as practised tends to separate makers from observers and thereby unintentionally suggests a sort of receiver psychology (Brown and Dissanayake 2009) that does not accord well with what we know about uses of the arts in pre-modern societies. We seldom know the *context* of rock art making or the circumstances (if any) of its later use, but if palaeoart is like the arts in other pre-modern societies, it may well have been associated with religious ceremonial practices in which music (instrumental and vocal), dance, costumes, masks and other 'artified' components were integrated (Dissanayake 2009). It is likely that most people were participants, not simply passive observers. Although they may not have made the markings and other visual elements that were part of the ceremony, group members may have felt intimately involved with them, as we do today in emotionally moving observances such as standing with others before the names carved on the Vietnam Veterans Memorial in Washington D.C. or in the candle and flower-strewn public spaces where people gather together after a natural or manmade disaster.

Evolutionary psychologists Larry Sugiyama and Michelle Scalise Sugiyama (2003: 182) remind us that costly signals may operate 'on several frequencies, capable of sending a variety of messages'. Thus the extravagance of inscribing rock surfaces, like time-consuming preparation of ritual spaces or paraphernalia (e.g. masks, costumes, musical instruments, arduous performances and elaborate scarifications) need not be interpreted only as costly signals for attracting mates or only as unfakeable proof of commitment, but also as 'indexical' of or correlative to the importance to individuals and groups of their beliefs and practices (Tambiah 1979).

These comments may seem harsh but I emphasise that I found the article to be informed, stimulating, and well worth publication. It tries to cover perhaps

too much ground although, as someone who has been writing about this material for several decades, I know that there are numerous relevant interlocking components of the complex subject of the origin and evolutionary trajectory of human art-making.

One especially important and useful contribution of the article is the collation from several sources of a large number of 'pre-artistic' aesthetic psychological adaptations that have been unconsciously co-opted by artists to catch viewers' attention (see the section before the authors' conclusion and occasional other mentions in their article). Some of these primary features relevant to palaeoart include humanly interesting subject matter such as animals (both predators and prey) and human figures (Thornhill 2003: 27); others have to do with graphic conventions for better identification of subject matter (Cheyne 1993, 2009), perceptual biases (Eibl-Eibesfeldt 1989b; Ramachandran and Hirstein 1999); others are formal, such as my own 'protoaesthetic operations' (Dissanayake 2010). As the authors point out, many of these adaptive preferences have been identified by more than one researcher, probably without knowing about each other's work. A further study that could better codify and discuss them would be of value to the field of evolutionary aesthetics.

To conclude, I am gratified to find that young and informed scholars are showing interest in the place of the arts in human evolution. I am pleased that the authors take trouble to dispel some common misinterpretations about the role of evolutionary explanations for human behaviour and I applaud their aim of opening an opportunity for multidisciplinary dialogue.

Acknowledgment: I am grateful to Ekkehart Malotki for generously providing invaluable assistance with palaeoart terminology and references.

Ellen Dissanayake
School of Music
University of Washington
Seattle, WA 98195-3450
U.S.A.
E-mail: edissana@u.washington.edu
www.ellendissanayake.com

RAR 28-1012

Generalised bundles and other perils in developing evolutionary aesthetics

By DUNCAN CALDWELL

The authors have two aims:

- To clarify evolutionary explanations for human behaviour by resolving common misinterpretations.

- To present a proposal that a 'co-evolutionary process of sexual selection ... shaped the design features of both rock art images and their aesthetic cognition by conferring mutual benefits on both producers, via manipulation, and receivers, via information extraction'. The authors propose to show 'techniques identified in rock art and [the visual] art[s] that indicate the occurrence of this co-evolution between producers and receivers'.

The article achieves both goals mainly by synthesising work by others. While such syntheses may be valuable for orienting future research, they run several risks:

- The first is oversimplification, which may lead one to disregard exceptions and alternatives.
- Another risk run by broad hypotheses, which have not been tested — and the authors do not pretend to have tested theirs yet — is the uneasy feeling that readers get when arguments proceed backwards: working from generalities towards particulars (especially when particulars remain largely absent). Without a tested foundation, an increasing load of generalities tends to make one queasy.
- A third temptation when an argument is distilled from existing writings is to make it appear seamless by citing a plethora of writers, sometimes without sufficiently weighing the merits of their work.

Let us delve into particulars. The first worrisome assumption in the article occurs when the authors promise to 'present a suggestion' based on 'the iconographic motifs universally found in rock art ...'. 'Universally' is such a broad word that it raises a red

flag.

Next, the authors plan to connect 'these traditional ideas with recent evolutionary approaches' — when the only 'traditional ideas' they have mentioned are rock art's 'universal' traits and Aristotle's proposal that all art imitates natural forms. We have to take it on faith that the universal features to be described later will stand up to scrutiny.

A bit further, the authors conceive of aesthetic evaluation as a 'spectrum ... from our enjoyment of beauty to our aversion to ugliness' and then ask us to '[n]ote that aesthetic processing is conceptualised as a phenomenon on a psychological continuum with both positive and negative extremes'. This polarisation of aesthetic appreciation is so caricatural that it is not surprising when the authors stumble in the next sentence: 'Thus', they tell us, 'negative emotions such as aversion and disgust are just as much aesthetic emotions as are wonder and elation'. If the continuum has both wonder and elation — two separate outcomes — at one end, not to mention other feelings, then the linear metaphor crumbles. Furthermore, what happens to the authors' simple continuum when wonder does not coincide with conventional notions of beauty? For example, Maou masks of the Koma secret society in the Ivory Coast (Fig. 1) are made to be as grotesque as possible, which may incite both revulsion and awe — and, to Western collectors, an acute sense of an emotional charge that they associate with their own notions of beauty.

Moving to a citation, Chauvet's lions might have roared in protest at being left out of Thornhill's 'adaptations for the aesthetic valuation of ... non-human animals, mostly for consumption (fish, ungulates, certain rodents and birds) or safety from predators (un-alarmed birds or ungulates calmly grazing) ...'. Luckily, the authors note the absence of '... many important aesthetic experience domains ...' — including that of predators and '... cues of neoteny (infantile traits) ...'. Just when I felt relief that predators had not been forgotten, this unexplained reference to 'neoteny' baffled me.

Are the authors referring to an un-stated hypothesis that such adult predilections as seeing faces in amorphous shapes are heterochronic retardations of what were just infantile preferences for looking at 'attractive faces' and erect T shapes that resemble faces, rather than inverted ones? After reading the paper, I am still not sure what 'neoteny' referred to here. Furthermore, I do not know of any evidence that adult visual preferences are heterochronic.

My major concern, though, concerns the paper's biggest leap: '... we can consider that human beings have a stable intellectual, imaginative, emotional and aesthetical nature that is universal across epochs and cultures'. It is one thing to say that there is such a thing as 'human nature' because of the genes that humans share, but it is another to make that commonplace the basis for a scientific argument. When one does, one



Figure 1. Maou masks of the Koma secret society, Ivory Coast. Quai Branly Museum, inv. 73.15583.

must be careful to avoid including anything that is not actually universal. But the authors take the risk when they announce their intention 'to draw attention to the universal prevalence of a specific set of general motifs, such as human-like figures or animal-like figures'.

They then proceed to compile short lists of motifs found in eight countries or continents — Palaeolithic Europe, Norway, Italy, Spain, Botswana, China, Brazil and Australia — that sweep regional and temporal differences under the rug. Such generalised bundles give the impression that certain motifs like anthropomorphs or zoomorphs are indeed universal and are even 'themes', when, for example, they are absent from all but a tiny fraction of the richly engraved rockshelters and caves in the Massif de Fontainebleau from the Mesolithic through the Bronze Age (Fig. 2). That single exception is so geographically and temporally huge as to beggar words — and is far from unique.

The same corpus also flies in the face of the authors' argument that they can 'identify the co-opting of aesthetic appreciation related to' one of the 'four pre-existing aesthetic adaptations listed by Thornhill ... apparent social scenarios'. Just as social vignettes seem almost entirely absent from the Palaeolithic canon in Europe (with such rare exceptions as the Magdalenian '*Rangée d'individus marchant*' from Gourdan and a late frieze from Addaura, Sicily), there is not one identifiable pre-Historic social scene among the 1200 known art sites in the Fontainebleau region. Such big exceptions should put that particular universalism to rest.

The Fontainebleau corpus also illustrates a geographic problem with the authors' arguments since almost the entire inventory, stretching over many millennia, is found on one side of a narrow river, the Loing, although the same rock formations and cavities exist in abundance on the other side. Similar gaps in the supposed universalism of rock art exist elsewhere, for example in the Iroquois heartland, where rock art is almost entirely missing, despite its rockiness, while the surrounding Algonquian zones often have rich rupestrian traditions. Yet both the Iroquois and Algonquians are simply the latest of a series of cultures in their respective areas, meaning that the gap actually covers more phases than the historically known ones. Such huge lacunae, spanning many shifts, need to be explained before one gets carried away with lists of things that are visible when one is so far away from the details that most of them have been eclipsed.

Around this point, the authors claim that they 'have presented the plausible origins of our aesthetic cognition involved in the visual arts, focusing on rock art co-opting existing cognitive mechanisms ...'. I admit that they have made an effort, but it seems to fall short of their pretensions.

Next, the article approvingly cites a study that equated the observational accuracy of 'primitive artists' with those of 'children ... especially for figurative representations'. The more one knows about the com-

plexity and variety of imagery produced by modern hunter-gatherers and tribal cultures, the warier one is likely to be of using such a misguided word as 'primitive' for almost any of it. Take Nkisi Nkondis, for example. Europeans have held these so-called nail fetishes up as the epitome of 'primitivism' since the Portuguese explorer Diogo Cão first made contact with the Kongo in 1483. Yet the statues are easily as complex in their iconography and as dense in their aesthetic choices (McClusky 2002) as most modern Western masterpieces, the Magdalenian '*femme au renne*' (Caldwell 2010a, 2010b) or the Chauvet '*Venus*' and her consubstantial bison consort.

Luckily for the authors, the second half of their paper, where they finally present their hypothesis concerning sexual selection, is more carefully argued. But there are still some flaws. For example, the authors mention that '[I]ndividual style serves to enhance a positive self-image and suggests that a person is industrious ...'. I wonder if they meant to refer to 'individual display' rather than 'style', since innovation is frowned upon in many cultures that place a premium on social cohesion and learning from elders with high fidelity. Display, within established limits, may be encouraged, though.

Further on, the authors argue that rock art 'must be easily observable by most people' 'to qualify as a costly

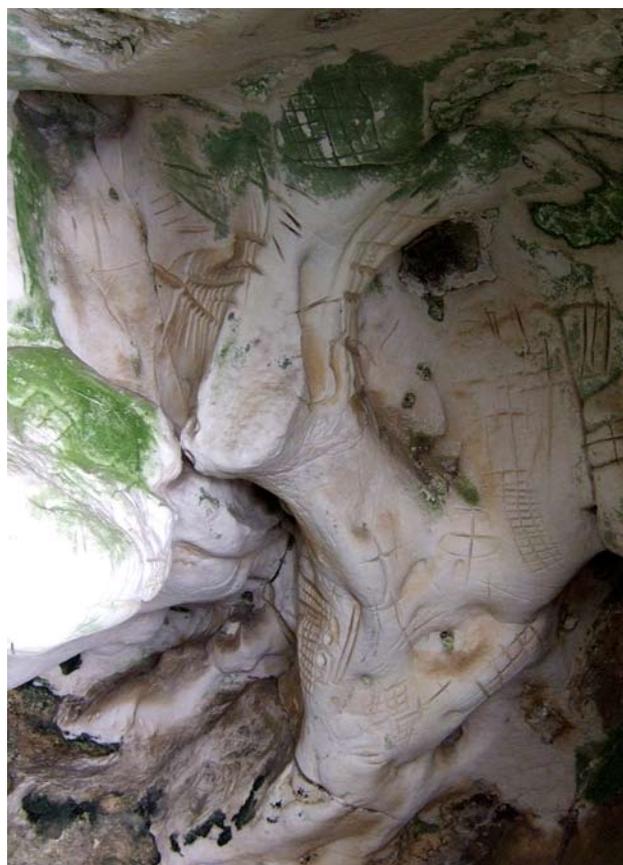


Figure 2. *La Grande Montagne 1. A fairly typical cavity in the Trois Pignons forest, Massif de Fontainebleau with a plethora of grids and other abstract patterns.*

signal ...'. While rightfully lauding Villeneuve's thesis, which showed that larger, more complexly pigmented cave imagery tends to be more accessible than simpler parietal images, the authors jump to the conclusion that this means that such imagery had larger audiences, which, although probable in some cases, is far from proved for many of them. In some cases, more accessible spots may have simply been more convenient for the image-makers themselves. Furthermore, the contention avoids two bothersome facts illustrated by Pech-Merle: one, the images are not easily observable in their larger context, deep within karstic caves, where they are sometimes even reached by the narrower of two or more passages; and, two, areas that were conducive to the preservation of footprints attest in some cases to the limited number of Palaeolithic visitors. The friezes at Cap Blanc and Roc-aux-Sorciers are easily observable and make good candidates for costly signals, but the definition will have to be refined before it can be applied to deep cave art. In some cases, the highly observable aspect of the artist's effort may have been his preparation and departure into the underworld, not his actual production, forcing us to integrate those phases into the notion of costly signalling.

While showing one aspect that might have been selected for sexually — skill — the deftness of much parietal art, which indicates that it was often done quickly, also undermines the costly signal hypothesis unless one integrates the journey into the cave into the equation.

A similar problem arises with the authors' contention that rock art complies with costly signalling predictions because of the artists' frequent 'access to resources made from rare or expensive materials (pigment composition) ...'. While the use of imported pigments exists in such art produced for large polities as the Mayan friezes at Bonampak, the pigments used in pre-Historic Saharan and European art were often obtained in the immediate environs.

Finally, I was intrigued to note that Cheyne et al. (2009) had shown that the horns in Palaeolithic illustrations of bison were twice as big as those of present bison. At least three factors could have contributed to this: the one approved by the authors, which is that the horns show caricatural exaggeration; two, selective hunting of large specimens in recent millennia, leading to diminished horns in modern bison — which would echo the extinction of *Bison antiquus* and the reduced horn size of American big-horn sheep due to selective trophy-taking; and, three, the fact that some Palaeolithic bison imagery played on similarities in the contours of bison and mammoths, leading artists to exaggerate some horns to make them resemble tusks (Caldwell 2010b; Howley 2010).

To sum up, this article leaves me ambivalent. On the one hand, the compilations near the end are useful, the subject is important, and references to Grill-Spector et al. (2001), Cheyne et al. (2009) and Villeneuve (2008) provide some bricks for a foundation. On the other

hand, the article rests partly on fudged data sets and such unstable and simplistic polarities as 'beauty' and 'ugliness'. As we have seen, almost the entire corpus of pre-Historic engravings from the Massif de Fontainebleau, for example, is so abstract and hermetic to modern observers that the markings escape the figurative criteria for perceiving 'beauty' used in the article, suggesting that most of the engravings might be classified as 'ugly'. What a shame for the reproductive hopes of their makers!

So where can one go from here? First we must seek the design archetypes that might have been selected with greater subtlety, something explored by Barbara Olins Alpert in *The creative Ice Age brain* (2008). Secondly, patient research has to be done to collect data that could support the 19th century hypothesis that sexual selection affected the evolution of visual aesthetics. Given the existence of ethnic groups who produce visual art in the same environments as related ethnicities that do not (for example in southern Burkino Faso), it would be interesting to know if people with a visual tradition have larger families, higher population growth, or anything else of the sort — and if the artists of various visual traditions produce more offspring than non-artists in their communities.

But such research is not for the faint of heart, because problems and counter examples loom so large. Take the blacksmiths of many Bantu peoples, for example. They produce much of their peoples' imagery — whether in wood or metal — but are often forbidden from marrying outside their shunned castes. Needless-to-say, this may create problems for the sexual selection and dispersal of the artists' traits. So while I admire the authors' effort and am sure that sexual selection has indeed affected the evolution of some aesthetic predilections, more encyclopaedic knowledge and insight must be brought to bear to refine the argument.

Duncan Caldwell
Marine and Paleobiological Research Institute
18, rue Rambuteau (B35)
75003 Paris
France
E-mail: paleothought@yahoo.com
RAR 28-1013

Arts and the peacock's tail that wagged evolutionary aesthetics

By AHMED ACHRATI

The article by Varella et al. aims 'to clarify the role of evolutionary explanations for human behaviour by resolving many common misinterpretations', and 'to present a theoretical proposal elucidating ways in which evolutionary processes might have shaped

aspects of our artistic cognition involved in visual arts, especially rock art'. Following Miller and Dutton, the article attributes the origin of art to sexual selection, then proposes a 'demonstration of how our artistic appreciation emerged from ancient non-artistic aesthetic appreciation, coevolved with art production, and of how strong were the selective pressures acting on this new artistic aesthetics'.

A few observations on a basic understanding of evolution are in order before my comments on the merits of this evolutionary view of aesthetics.

Sahlins, Velden and others have decried the tendency of some sociobiologists and evolutionary psychologists to explain evolution, an 'idea of differential reproduction dependent on chance genetic and environmental shifts', by reducing natural selection to a theory of optimisation of individual genotypes (Sahlins 1978: xiv; Velden 2010: 31). This criticism is justifiable in view of the ambiguity of 'natural selection' and its misuse, which Darwin himself was aware of:

Thus a large yet undefined extension may safely be given to the direct and indirect results of natural selection; but I now admit ... that in the earlier editions of my 'Origin of Species' I perhaps attributed too much to the action of natural selection or the survival of the fittest ... Any one with this assumption [that every detail of structure, excepting rudiments] in his mind would naturally extend too far the action of natural selection, either during past or present times. ... [H]ence if I have erred in giving to natural selection great power, which I am very far from admitting, or in having exaggerated its power, which is in itself probable, I have at least, as I hope, done good service in aiding to overthrow the dogma of separate creations (*Descent of man*, 100–101).

It did not help that Darwin used another term, 'preadaptation', to describe the transformation of biological structures and behaviours from one use to another, 'since it can too easily be misunderstood to imply that somehow evolution 'knows' what structures will be useful for future descendants of the current organisms' (Cziko 1997: 56). Sometimes selection is even assigned a contradictory role, always preserving traits only to eventually kill them off (Velden 2010: 32).

All this has endowed 'natural selection' with an *active* agency of fitness — a force targeting useful biological traits in order to foster them. Hence the ongoing debate on *aptation*, adaptation and *exaptation* (Gould and Vrba 1982; Parker and Jaffe 2008: 23–24).

Empirically, however, as our daily lives teach, 'selection' exhausts its meaning in its eliminative effects. Take two selective processes: apples on a conveyor belt and a Baccalaureate exam. They tell us nothing definite about the items being evaluated except which apple or student has failed passage. They tell us nothing about whether an apple will be in a child's lunch box or in an apple pie. Nor do they tell us what a graduate student will become, a scientist or a lawyer. This is where evolution and adaptation, not 'selection',

come in.

Humans are products of evolution; extinct hominins are evidence of natural selection.

This is why Darwin speaks of evolution in terms of grade and 'species that graduate', letting natural selection be the corrosive force that it is, carving the empty spaces between the dendritic arms of the evolutionary tree.

A case in point in the over-reaching of natural selection is the article's uncritical acceptance of the 'handicap principle' as an evolutionary explanation to the phenotypic tail of the peacock, which is proposed as model for sexual selection. Basically, to be a believable and inimitable mating signal, the peacock's tail (and similar sexual ornaments), come with a cost (Zahavi and Zahavi 1997).

As Pomiankowski and Iwas (1998) have shown, there are many problems with the 'handicap principle'. There is, however, one defect in this economic analysis of evolution which has yet to be pointed out: the 'handicap principle' accounts for the cost of the peacock's tail to the male of the species, but fails to account for those costs that are more relevant to evolution of the peafowl species as a whole; namely, by investing in its ornamental tail, the peacock burdened not only itself but also its whole species with even greater costs:

1. The species forewent a uniquely avian adaptive opportunity: *control of time* (seasons) through the use of long range flight/migration to various environments (e.g. cranes, eagles, flamingos).
2. Dependence on a given territory reduced the chance of peafowl's species variation; only two species of peafowl exist (*Pavo cristatus* and *Pavo muticus*).
3. High exposure to extinction of species that invest heavily in male ornaments (e.g. *Megaloceros giganteus* and *Bubalus*).

Adding to the ambiguity of selection is a loose definition of fitness (e.g. 'inclusive fitness' in Zahav and Zahavi 162) and its excessive focus on genes and the organism. Evolution is the change in the relative frequencies of the genes that determine the traits of the organisms of an entire population. But, as Velden (2010: 32) pointed out, if fitness is to be 'the degree to which the organism is more capable of reproducing', then the 'reproduction strategy' should include 'all behavioral aspects [that] are of relevance that can contribute to survival up to the reproduction age (this is what one usually thinks of in connection with Darwin's term 'struggle for life'), to the finding of a partner (or many partners), to fertility in combination with this partner, and to care for the survival of the descendants up to their age of reproduction' (Velden 2010: 32). In most species, humans included, this fitness is more satisfied in the female and less in the male.

But a more significant problem with the article is that it links artistic creativity, sexual display and mating choice, but ignores the role of pleasure in the creation and appreciation of art. The reason the article does not

discuss pleasure, I suspect, is the paradoxical connection between creativity, pleasure and mental disorders (Andreason 2005: 95–96; Miller 2009, 2001; Nettle and Clegg 2005). Indeed, one of the underlying causes of a mental disorder such as schizophrenia, neurologists have concluded, is *anhedonia*, or the loss of the capacity to experience pleasure (Andreason 2007; Andreason 1997; Kringelbach 2009). Interestingly, Miller, whose views provide the foundation of this article's assertions, did address the issue of mental disorders and artistic creativity as a sexual fitness indicator, but his solution to this paradox is not congenial with the article's thesis: Miller simply operationalised schizophrenia as a minor fitness indicator complementing the good genes, now an evolutionary gift to the relatives of the mentally-afflicted person (Shaner et al. 2008: 194; Nettle and Clegg 2005).

Nor does the article address the correlation between creativity and homosexuality, which some evolutionary psychologists have reduced to 'inclusive fitness' (Gautam 2001), instead of simply the obvious, that freedom and the pursuit of pleasure are the evolutionary achievements of humans.

Yet freedom is clearly implied in the key terms this article uses: 'preference' and 'choice'. From an evolutionary point, one can argue that freedom is a loosening of survival pressures that accompanied our neurological development, which decreased our dependence on the environment and kinship groups, diminished the survival value of technical behaviour (Oldowan tools) and increased our ornate/aesthetic behaviour (Acheulian tools). Reduction in survival pressure was also accompanied by a rise in self-awareness, self-assertion and a need to expand the outlets for the freed pleasure drive. Creativity became a fitting outlet for the pleasure drive and the newly-found freedom, and so was mate choice. Being low on creativity, mate choice behaviour availed itself of art as a prop for fitness but was not responsible for its existence. Art did not evolve as an epiphenomenon of other behaviours, 'but as a positive and primary motivation in its own right' (Sousa 2004: 111, quoting Dissanayake). Furthermore, as Feist has suggested, art has no survival value but could be given reproductive significance (Feist 2007: 17).

Unfortunately, freedom is rarely and inadequately discussed in evolutionary literature. Ansermet and Magistretti (2007) explored the evolutionary idea of freedom, but only to seek biologic determinants of the unconscious. And Edelman (2006: 99) is sceptical. For him, creativity involves originality, inventiveness, expressiveness, imagination, production, construction and making. 'Less obvious', he says, 'is the implication that a creator has freedom to create, connecting the various aspects of creativity to problems of free will' (Edelman 2006: 99).

Yet the key concept in the stated proposition of the article under consideration here is the appetitive word, 'preference', implying both pleasure and freedom

('Darwinian aesthetics will achieve explanatory power [for art forms and adaptations] ... by showing how their existence and character are connected to Pleistocene interests, *preferences*, and capacities.')

Pleasure is crucial to art and cognitive development. As an appetitive behaviour, art is naturally displayed in children's activity (Bednarik 2008a; Guthrie 2005; Dutton 2010). In fact, Bednarik and Guthrie believe that some of the Pleistocene art is the product to children. J. Huizinga (1956) even defines humans as *Homo ludens* on account of our child-like pleasurable and playful pursuits.

In this respect, and with rock art being the focus of the article, the story of Giotto di Bondone is quite illuminating. As a child herding sheep, this first true Renaissance artist was continuously drawing on stones and the sand of things he saw or fancied (Vasari et al. 1998: 15).

Equally instructive is the life of Charles Schultz, the creator of the cartoon 'Peanuts', especially with respect to the assertion of art as primarily a sexual fitness signal. Through his artistic pleasure in childhood, Schultz became a dominant artist in many media. Yet, looking into Schultz's *High school yearbooks*, his biographer found that his art brought him no feminine attention (Michaelis 2007: 106). In fact, a sample of *High school yearbooks* could provide a good test for the article's hypothesis on the 'sexual success' of artists.

What is disturbing about Schultz's experience, though, is that as his daughter began to draw cartoons, imitating her father, he told her, 'They are good', but then 'let her know that he wanted one of his sons to carry on his comic strip' (ibid. 374–375).

Conclusion

Like the colour of our skin, language and art are the products of evolution. So is human freedom, which the male, like the peacock, has up till now selfishly used to enhance his ornaments, transforming our evolutionary gifts into 'cultural construct[s] devoid of explanatory power' (Jablonski 2004: 615; cf. Aoki 2002), even a justification for slavery, misogyny, colonialism. Connecting evolution, art and male sexual behaviour, as this article seems to do, ignores the fact that evolutionary reproduction is primarily a maternal function (Dissanayake 2007, 2000b; Coe 2007), and risks giving patriarchy the endorsement of science, a job already taken by religion.

Dr Ahmed Achrati
School of Continuing Education
Georgetown University
Washington, D.C.
U.S.A.
E-mail: aachrati@gmail.com

Aesthetics and sexual selection

By ROBERT G. BEDNARIK

It would be great if this endeavour of Varella et al. (henceforth 'the authors') to bridge the gap between scientific and non-scientific disciplines (humanities) could succeed, but those who have tried this in the past have found the gap unbridgeable. The two sides exist in different realities (Sapir 1929). Although the authors bring an impressive array of theoretical constructs to their task, such as co-evolutionary theory, as well as a great deal of enthusiastic and very well argued reasoning, their hypothesis falters when considered critically.

The concept of rock art aesthetics, correctly mentioned by the authors as being 'of our sensations of anthropogenic marks on rock' (my emphasis), is of no relevance to rock art studies; it clearly belongs in a discipline of the *study of present-day rock art viewers* who have no cultural connection with the marks on the rock surface. The vibes of archaeologists (or other beholders of images on rocks), about the aesthetic properties of this imagery, are therefore of interest only to a psychologist who studies archaeologists. The authors' notion 'that human beings have a stable intellectual, imaginative, emotional, and aesthetic nature that is universal across epochs and cultures' is not only presented without justification or evidence, it is contradicted by their own previous observation that notions of beauty differ greatly between different societies (which is indeed the case; they may also differ between individuals of the same society). A predisposition is either universal or not; it cannot be both. At best we can rationalise that notions of beauty differ among societies, and to a smaller degree among their individuals, but they may also be completely absent in conspecifics. The authors try to explain this 'anomaly', but I am tempted to see such gradations in much the same way as I view human susceptibility to pareidolia (which the authors touch upon all too briefly): it varies greatly from one individual to the next, although it seems to be near-universal among extant humans.

Aesthetics, according to the authors, spans reactions ranging from those of apes (reacting to spectacles of nature: waterfalls, sunsets, heavy rain etc.) to those elicited nowadays by the fine arts. I am troubled by the connection the authors seem to perceive between 'ancient non-artistic aesthetic appreciation' and its modern counterpart. The modern constructs of both art and aesthetics are historically recent inventions, rather like the notions of nation-state or archaeology: there is no evidence that they would have had any currency in the distant past. The perhaps greatest complication with palaeoart, including rock art, derives precisely from its perceived connection with 'art'. Art, a concept lacking a universally agreed scientific definition, lumps together everything from a Beethoven sonata to an engraved

ostrich egg. Does art-like production by other animals, ranging from primates to elephants, have aesthetic dimensions for these species? In view of the authors' impressive opening of this line of enquiry, I would welcome their exploration of this issue.

The 'costly signalling theory' is ethologically significant, certainly, but its connection with the 'aesthetic qualities of animal ornamentation' is based on a falsity, an anthropomorphisation: there is no justification for assuming that the peahen's appreciation of the peacock's tail feathers is aesthetic. The perception of it being aesthetic is very probably limited to humans. Most costly signals involve no elements we interpret as aesthetic: would we think of aesthetics if the peacock's costly signal were to jump like an impala?

Is there an adaptive value in aesthetics? Since, as the authors contend, negative emotions such as aversion and disgust are just as much aesthetic emotions, is the disgust or alarm I experience when I watch the slaughter of an animal — which would be an aesthetic aversion in the language of the authors — of adaptive merit? In Darwinian terms it would have to be maladaptive. The authors do 'expect to find many maladapted behaviours and by-products of exapted learning mechanisms', and most thoughtful people would agree that modern humans are the most maladapted species on the planet.

The authors' chapter on rock art can be summarised in a single sentence: there are vast numbers of rock art motifs in the world that have been 'identified' by thousands people who believe that they have some special ability of recognising what objects were depicted. But it is unclear how the great variety of purported identifications of objects is of scientific relevance, or how these translate into aesthetic significance. Most societies who produced rock art probably created much greater quantities of other art, while most primates — from the apes with 'ancient non-artistic aesthetic appreciation' to near-modern humans — have left us no rock art. Indeed, all of the rock art cited by the authors appears to be Holocene, and is therefore hardly of relevance to evolution, evolutionary aesthetics or sexual selection. I would strongly encourage the authors to reconsider their views in the light of Pleistocene palaeoarts, and most specifically those of the Middle Pleistocene.

In trying to make a case for rock art being a trigger for sexual selection we need to recall that a great deal of rock art is sacred and is typically related to gender-exclusive activities, ranging from sympathetic magic (e.g. increase ceremonies) to malevolent sorcery and to ceremonies categorically excluding the opposite sex. Clearly it cannot be a display to facilitate sexual selection. Similarly, much rock art is made in solitude, be it on vision quests or in such narrow spaces that no audience could have possibly been involved. In many cases large motifs occur in such restricted spaces that even the artist could not see the whole image. Although the accounts provided by living societies

with traditions of rock art production should not be projected onto earlier cultures, neither should they be ignored. They show overwhelmingly that, just as in modern society, some individuals were more artistically inclined than most, and typically they were the most prodigious producers of traditional 'art' forms. I am not aware of any evidence, or even suggestion, that these individuals had more offspring than their contemporaries. Nor were most of the greatest artists of Western history — composers, painters or whatever — particularly fertile. It may even seem that many remained issueless, perhaps precisely because of their magnificent obsessions. A potential variation to the authors' position would be that it might not be the individual, but the group as a whole that acquires the selective advantages they suggest, but then the argument in favour of sexual selection evaporates.

The statement 'given the importance of evolution for understanding human nature, in particular with respect to rock art expression and appreciation' invites further comment. Human nature today is mostly not the result of evolution. Natural selection has long ceased to be relevant to us, because for some tens of millennia we have been shaped largely by self-domestication (Bednarik 2008b): Mendel, not Darwin, has determined our trajectory since sexual selection has become culturally moderated. Whilst I am not sure which 'cues of neoteny' relate to aesthetics, this term is a cue for me to address human neoteny, and to hopefully point the authors into a different direction. Two issues deserve close attention: one is the proposition I have pursued for 25 years, that a significant part of palaeoart is the work of juveniles (Bednarik 1986): did children contribute to sexual selection? The other is even more relevant here.

A careful neutral examination of what are quaintly called anatomically modern humans reveals that rather than being the spitting image of a deity, they are neotenous apes, sharing most of their somatic characteristics with foetal apes; they are greatly inferior to their ancestors, robust *Homo sapiens* types such as the much maligned 'Neanderthals'. For instance they have significantly smaller brains, are far more liable to suffer cranial trauma and are physically much weaker. They are susceptible to several thousand genetic disorders not found in other primates, and very probably not in previous hominins. They are subject to numerous neurodegenerative diseases, mental illnesses, Mendelian disorders and many other detrimental conditions, the ascendancy of which is the 'side effect' of domestication by sexual selection (Bednarik 2011). Although obsessive traits first appeared in the Lower Palaeolithic, since the Late Pleistocene they have burgeoned to the point that today our existence is entirely governed by them; the sophistication of our modern culture would be impossible without behaviour that resembles clinical obsessiveness. For instance our obsession with wanting to believe in something, our search for meaning where there is in fact none and similar expressions

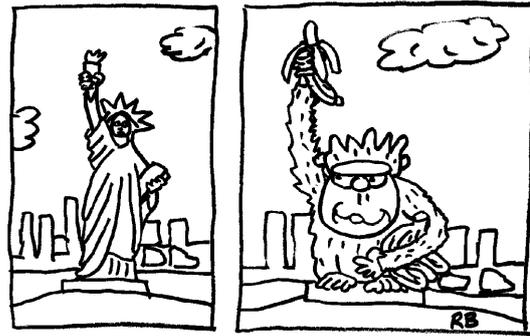


Figure 1. Cartoon by Robert Bednarik jun.

of our neuroticism are all irrational. No other primate could be bothered with them (Fig. 1), or with pursuing excellence, e.g. by improving sleeping nests or tools; yet for humans the pursuit of perfection has become an obsession. Most of what we do every day of our adult lives is in fact either irrational or obsessive — and often both.

Human self-domestication (Bednarik 2008b, 2011) by sexual selection should be of considerable interest to the authors, because it very probably involved aesthetics. A principal variable of selection was attractiveness, which would have had to be based mostly on arbitrary cultural constructs. An exception might be facial symmetry, which may express immunocompetence (Grammer and Thornhill 1994; Shackelford and Larsen 1997), but sexual selection on the basis of youth, specific body ratios, facial features, skin tone, hair and similar factors, strongly established in modern humans, is completely absent in other primates, or indeed in all other animals. In female humans neotenous facial and other features are strongly preferred by males (Jones 1995, 1996), which drove selective breeding since mid-Würmian times (Bednarik 2008b, 2008c), promoting dimorphism and rapid gracilisation. Mating preferences and their genetic results in respect of personality and anatomical traits (Laland 1994), which could become cultural selection variables, can be modelled by methods of the gene-culture co-evolutionary model (Cavalli-Sforza and Feldman 1973; Feldman and Cavalli-Sforza 1989; Aoki and Feldman 1991; Durham 1991). The autocatalytic process I have proposed involves the insertion of 'aesthetics' into mate selection that drove our domestication, impelled purely by 'invented' qualities. Just as the gracilisation of modern humans, unchecked by natural selection, involved the establishment of numerous unfavourable alleles, the formation of criteria of excellence facilitated their cultural (sexual) selection. Once encoded genetically, but not moderated by natural selection, the supporting neural system lacked the Darwinian defence system and detrimental variations developed. For instance in obsessive compulsive disorder, the pattern of repetitive firing in the error detector in the orbital frontal cortex and anterior cingulate is such a result of surfeit of

sentience (Bednarik and Helvenston in press).

In its present state, the hypothesis of the authors is not adequately formulated to encourage confidence in its empirical testing as proposed in the above paper. For instance, how is it envisaged to quantify the level of 'aesthetic discernment' among ovulating women relative to a non-ovulating control sample, and their inclination to 'view art-works as expressions of male talent'? To be persuasive such experiments would need to be designed to falsify the hypothesis rather than provide fully contrived support. Nevertheless, the authors have presented an excellent case for a much more comprehensive study, and they have provided a wonderful topic for a productive discussion. Evolutionary aesthetics or evolutionary psychology deserve the most meticulous consideration, but need to be situated in an all-inclusive, consummate framework. I would particularly encourage the authors to persevere with their endeavour of introducing advanced biological reasoning in the field of palaeoart origins, but to broaden the basis of their enquiry along the lines I have suggested.

Robert G. Bednarik
P.O. Box 216
Caulfield South, VIC 3162
Australia
E-mail: auraweb@hotmail.com

RAR 28-1015

REPLY

Approaches, concepts, universalities and sexual selection on the evolution of palaeoart appreciation

By MARCO A. C. VARELLA, JOSÉ HENRIQUE B. P. FERREIRA and ALTAY A. L. DE SOUZA

We, the authors, are pleased to see so many good comments about our paper on evolutionary aesthetics and sexual selection applied to rock art aesthetics. After almost two years of learning, exploring, developing and extending our argument, from our trip and talk at the IFRAO Congress in 2009 in Piauí, Brazil, to this reply, it is wonderful to realise that we have indeed succeeded in generating an interdisciplinary productive debate. In this regard we are grateful to *Rock Art Research*, the referees, the commentators, and the editor for taking so much interest in our paper and for this valuable opportunity.

After carefully reading all the various issues each commentator raised, we realised that if we were to

respond to each one, it would take us many weeks of background reading and several pages of reply. Instead, we have decided to comment on the most recurrent issues raised: our approach; concept of art and aesthetics; universalities; sexual selection. Other issues and any specific point not addressed here can be answered anytime by personal communication.

Our approach

Regarding our approach, we are glad that our referencelistandthe compilation of pre-artistic aesthetics and artistic operations were acknowledged. Yes, we are young, enthusiastic researchers, who lack both access to many journals and encyclopaedic knowledge on rock art. We agree that some references could have been more fully explored and connected, but we feel that our main argument was not prejudiced by that, and we did want to exchange those references with the reader as part of our 'endeavour of introducing advanced biological reasoning into the field of palaeoart origins' as stated by Bednarik. We are aware that we run the risk of oversimplification and also that it is hard to test some of our predictions, but we feel the discussion raised and the future possibilities are worth those risks.

We thank Watson for helping us to better understand his paper on doodles (Watson 2008). We agree that the cognitive biases we have mentioned can be seen as 'powerful triggers of neural activities underlying aesthetic responses', as he put it, and that most psychological aspects mentioned by us should also be traced to neural activity, areas and connective patterns. We then saw some interpretation issues about neoteny that needed clarification. We referred to the liking (or at least not disliking) of infant and juvenile forms, like big eyes and head, small nose, jaw and limbs, among others. So it is not about infantile aspects of adult appreciation, as Caldwell has understood, but only the widespread positive attribution of the infant schema, silhouette and proportions, as seen by Gould (1980) and Eibl-Eibesfeldt (1989a). We also want to clarify to Achrafi that we are ignoring the role of pleasure because we are concerned with evolutionary aspects, not proximate aspects. Proximate aspects, like pleasure or even motoric and neural pathways, are not alternative explanations, but a different way of looking to the same phenomenon. They focus on how things work now instead of why it has been that way in the population for generations. Both kinds of analysis are needed for us to understand palaeoart.

Concept of art and aesthetics

We note that Dobrez, Caldwell and Bednarik express concerns about our concept of art and aesthetics, in which regard Dissanayake gave a wonderful clarification of our point separating the ethological view from the philosophical one. We knew that in 'bridging the gap between scientific and non-scientific disciplines' as Bednarik put it, definitions would be the major problem.

Despite all the historical transformations and cultural variations of the meaning of the term 'aesthetics', from a psychological or animal behaviour point of view it all comes to a measure of preference/avoidance.

Our concept of basic aesthetics is that we have a single neurocognitive pleasure centre responsible for generating the 'liking' or 'disliking' final response regarding many different domains and sensory inputs. However, the specific set of rules, which is, of course, open to cultural influences, that processes the signal for a positive or negative response is different for each domain and sensory canal. This solves the problem identified by Dobrez of how the aesthetic dimension can be so diverse in its assessment, ranging from food to ideas, though essentially bi-dimensional in its basic response. Also this is only part of the story, since we have expectation mechanisms and emotional reactions instantly interacting with and modulating in different ways every aesthetic judgment.

When it comes to art, it is true that Dissanayake's artification concept can solve many problems related to conceptions of 'high art', but if we had not used the word 'art' we would not have captured the interest of those studying arts and palaeoarts and we would have failed to create the interdisciplinary debate. The distinction between art as product, from artification as the productive behaviour, and appreciation as the aesthetic judgment of the behaviour and its product is essential indeed. Since our focus was on artistic appreciation there is no contradiction, as seen by Helvenston, in the fact that artification is a general behavioural adaptation relevant to all arts and our specific proposed adaptation of visual arts aesthetics. Many commentators have said that we focused too much on representative art and that abstract art was an inconvenient contrary fact. The unique difference for our argument between representative and abstract palaeoart is that the former co-opts aesthetic mechanisms that deal with concrete things, skills and ideas, and the latter co-opts aesthetic mechanisms that deal with perceptual patterns, regularities, and also skills and ideas. The entire sexual selection co-evolutionary process can occur in the same way for both cases.

In any case we are aware that the problem of what 'art' is and has been to our ancestors cannot be easily solved in a few paragraphs, given the complexity of the subject and differences of approaches in the humanities and sciences. It is important though to respect those different approaches and realise that as the humanities approach can be applied to scientific subjects, the scientific approach can also be applied to humanities topics without being exclusive in either case. The principal tension between these fields is that the weight given to particularities is much bigger in the humanities and the weight credited to generalisations is much bigger in the sciences. That is why that majority of the criticisms relates to the presentation of particular examples (places with traces of human ancient occupation and rock formation, but without rock art; ugly,

unskilled, non-original or hermetic abstract art; easy to get paint ingredients; deep-cave hidden palaeoart; women and children as the producers, and so on) as being the unforgiving exceptions for our rigid scientific general rule. That is also why the notion of universal human nature and any other universal aspect were not well received. We recommend papers on the philosophy of biological science by Mayr (2004) for a deeper understanding on how biology can be the science of the exceptions and at the same time a unified scientific field.

Universalities

The definition of things as universal is highly problematic when we are talking about human biology, psychology and culture. Some issues were raised about the universality of rock art motifs, appreciation judgments, and other psychological characteristics. We agree with what Caldwell pointed out, that the universality of iconographic rock art motifs need to be tested more carefully, focusing especially on older Pleistocene palaeoart, as Bednarik has emphasised. The fact that humanities are focused more on particularities inhibits the development of a comparative palaeoarts study by not allowing us to see the big picture and to test our kind of general explanations. And we are aware that all of those motif interpretations are biased by the view of the modern mind, which could influence the research outcome. However, it does not mean that only those interested in studying the psychology of archaeologists would be interested in present human reactions to rock art. An experimental psychology approach could help in this sense by accessing many psychological and physiological aspects of the present average human reaction to rock art, including its identification.

Dobrez and Caldwell have criticised the argumentation of a universal concept of beauty. As we have stressed in our paper, the concept of beauty that we use is related to the general capability to identify and define something as beautiful. We are not referring to a notion of beauty of a specific culture or individual, which could vary as result of different ecological conditions and historical facts. There is no contradiction in something being universal and varying culturally, because what we mean by universal is the propensity to ontogenetically develop something according to each environment. So the fact that humans have a language instinct does not imply that there would be only one spoken language in the world, the same for everybody; nor that it would not have any language disorders. We have universal cognitive rules underlying language processing which are open to environmental input. That is why we have all this cultural variation. It is the same with the aesthetic sense. Remember that the more each set of cognitive rules is open to environmental influence, the less universality is seen at the level of the manifest behaviour. This does not mean that there is no universality at a deeper psychological level.

Caldwell and Bednarik pointed out that the notion of 'intellectual, imaginative, emotional and aesthetical nature that is universal across epochs and cultures' is a not a well-grounded statement. As we argued before, in all cases we are talking about psychological mechanisms that underlie all of these human capabilities. Our psychological adaptations are sets of biases and learning propensities open to specific aspects of the developmental and contextual environment (Tooby and Cosmides 1989).

Buss and Greiling (1999) showed that individuals differ in innumerable ways and those differences could be adaptive, maladaptive or neutral. Variation could be the result of genetic, environmental changes during the gestational period, and childhood sensitive periods (early experiential calibration), and current environmental conditions. The easiest way to understand this may be by looking at adaptations as evolved strategies, an algorithm. Strategies typically are defined as genetically based programs (i.e. decision rules) that individuals use to allocate their somatic and reproductive effort to specific alternative phenotypes (i.e. mating tactics) in an adaptive way. In evolutionary psychology and behaviour ecology, behavioural variation arises as individuals match their conditional strategies to their diverse social environments (Buss 2009; Low 1998; Winterhalder and Smith 2000), which can explain variations from mating strategies (Gangestad and Simpson 2000) to personality (Buss 2009). As an example, sexual strategy is sensitive to environmental stability during childhood, to mortality rates, and to the relative frequency of men and women in the population (Gangestad and Simpson 2000; Schmitt et al. 2005). Many cross-cultural studies and reviews have shown universal patterns and their variations in a great variety of psychological characteristics, from sexuality (Schmitt et al. 2005), emotion recognition (Elfenbein and Ambady 2002) to facial expressions (Izard 1994).

Sexual selection

Regarding the sexual selection part of our argument, we are glad that our point that sexual selection is only one among several possibilities for the evolution of palaeoart was acknowledged. Needless to say, this entire part of the paper raised a lot of controversy. Some commentators created a false opposition between sexual selection and human culture and reserved sexual selection only for other primates and our distant ancestors. As demonstrated by our example of buying fancy cars and Bednarik's exposition of his self-domestication theory (Bednarik 2008b, 2011), any arbitrary cultural aspect can enter into the process of sexual selection; hence there is no exclusiveness between both concepts. Others created a false opposition between individual processes and group processes. Group selection, as the modern multi-level selection, is not an alternative explanation for art evolution from individual level simply because they are not exclusive; both processes can occur at the same time (West et al.

2008). At the same time that groups are competing with other groups for attention and being judged by their displays within or between tribes during rituals, individuals within each particular group are also competing and being judged. As for the displays in some birds even the individuals of each group are not regarded as having the same mating value; there is always a dominance hierarchy between or within groups, which at the end will pay off as differential reproductive access.

Still other commentators even created a false opposition between displays and same-sex activities, as if without a female audience there would be no sexual selection. It is important to remember that the image of sexual selection applied to rock art is not the one of finding engraved hearts with lovers' stick figures inside. Sexual selection is a process that encompasses the direct *and* indirect forms of male-male competition, female-female competition, males selecting females and females selecting males. And competition is not only crude fight, though even the fight in many animals is as ritualised as the mating dance and the ritualisation process in Dissanayake's theorisation about art (Dissanayake 2007, 2009, 2010). Some also indicated that our argument implied that only the ancestral males doing art would have reproductive success. Any activity, from hunting and fishing to cooking and cutlery making, from gathering, history telling to preparing healing potions and instruments or costume making, opens a social niche. In each of these social niches individuals and groups can specialise, raise the standards, hide know-how techniques and places of raw materials as sacred secrets, control the innovation level, create a hierarchy based on skill or any other criteria, and display its products, especially displaying the result of that particular hierarchy to others. In knowing this one can understand, among other things, why some forms of arts are meant to frighten instead of please, since part of the ritualistic fight is meant to intimidate others, and one can see that both male and female can display and appreciate displays of others, no matter which sex is displaying and on what domain. This also fits perfectly on Bednarik's theory of self-domestication in humans (Bednarik 2008b, 2011), which we will surely read more about in the future. However it does not mean that because of that there is no evolution happening with humans.

We would like to thank the comment by Watson regarding the authorship of rock art. As in most other species in which the females invest more in the offspring, males are responsible for most fights and other displays of hierarchy, resource and appearance. Especially young males with not much to lose are the ones more prone to the higher risks and costly behaviours (Daly and Wilson 2001). Of course this does not mean that *only* young males would have produced rock art, but simply that they would have had the higher motivation to do so. In our species male investment in the offspring is much higher than the average primate. This would set the

scenario for a more monogamous mating system with fewer sex differences, but there would still be some. Regarding the comment that if rock art were made by children our argument would collapse, we would like to mention that, as Geary (2002) has put it: 'many sex differences in peer relationships and play mirror adult forms of intrasexual competition (...) consistent with the sex difference in parental effort, girls engage in play parenting and other forms of family-oriented play much more frequently than do boys (...) boys engage in ecologically related play and other related developmental activities, such as exploration, much more frequently than do girls' (Geary 2002: 86). So we would not be surprised if one discovered that some rock art was clearly made by children.

We thank Caldwell for the suggestion about the inclusion of the preparatory phase in the equation of the cost of rock art, especially before the artist goes to deep and dangerous places. And we thank for the suggestion of the use of artists' biographies to test some of the predictions from sexual selection. Some of that has been already done for scientists (Kanazawa 2000), musicians (Miller 1999) and poetry writers (Lange 2010). And the results indicate that more males and unmarried ones in the beginning of their adulthood are the ones producing more and high quality displays, which open more reproductive opportunities.

All that said, we authors are honoured to be part of this select group of thinkers discussing the fascinating theme of palaeoart and its connections with and implications for different fields of study. We also felt stimulated and moved by this discussion. All the motivating words have made us want to keep learning and researching more about arts and palaeoarts, always broadening and refining our argument, and to keep creating fruitful discussion opportunities like this.

Marco A. C. Varella, José Henrique B. P. Ferreira and Altay A. L. de Souza

RAR 28-1016

REFERENCES

- ADAM, L. 1963. *Primitive art* (3rd edn). Cassell, London.
- AIKEN, N. E. and K. COE 2004. Promoting cooperation among humans: the arts as the ties that bind. *Bulletin of Psychology and the Arts* 5(1): 5–20. [ED]
- ALCOCK, J. 2001. *Animal behavior: an evolutionary approach* (7th ed.). Sinauer, Sunderland.
- ALPERT, B. O. 2008. *The creative Ice Age brain: cave art in the light of neuroscience*. Foundation 20 21, Providence. [DC]
- ANATI, E. 2008. The way of life recorded in the rock art of Valcamonica. *Adoranten* 8: 13–35.
- ANDERSSON, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.
- ANDREASEN, N. C. 1997. 'O brave new world! Exploring the mind and brain in health and disease. A Presidential Lecture, <http://sdrclib.lib.uiowa.edu/preslectures/andreasen93/index.html> [AA]
- ANDREASEN, N. C. 2005. *The creating brain*. Dana Press, Washington, D.C. [AA]
- ANDREWS, P. W., S. W. GANGESTAD and D. MATTHEWS 2002. Adaptationism — how to carry out an exaptationist program. *Behavioral and Brain Sciences* 25: 489–553.
- ANSERMET, F. and P. MAGISTRETTI 2007. *Biology of freedom: neural plasticity, experience, and the unconscious*; transl. by S. Fairfield. Other Press, New York. [AA]
- AOKI, K. 2002. Sexual selection as a cause of human skin colour variation: Darwin's hypothesis revisited. *Annals of Human Biology* 29(6): 589–608. [AA]
- AOKI, K. and M. W. FELDMAN 1991. Recessive hereditary deafness, assortative mating, and persistence of a sign language. *Theoretical Population Biology* 39: 358–372. [RGB]
- BATAILLE, G. 1980. *La peinture préhistorique: Lascaux ou la naissance de l'art*. Skira, Geneva. [LD]
- BEDNARIK, R. G. 1986. Parietal finger markings in Europe and Australia (with comments). *Rock Art Research* 3: 30–61, 159–170. [BW] [RGB]
- BEDNARIK, R. 1993. European Palaeolithic art — typical or exceptional? *Oxford Journal of Archaeology* 12(1): 1–8. [ED]
- BEDNARIK, R. G. 2003. A figurine from the African Acheulian. *Current Anthropology* 44: 405–412. [PAH]
- BEDNARIK, R. 2006. Neurophysiology and palaeoart, Toronto lecture No. 6: <http://projects.chass.utoronto.ca/semiotics/cyber/rbednarik6.pdf> [ED]
- BEDNARIK, R. G. 2008a. Children as Pleistocene artists. *Rock Art Research* 25: 173–182. [BW] [AA]
- BEDNARIK, R. G. 2008b. The domestication of humans. *Anthropologie* 46(1): 1–17. [PAH] [RGB] [VFS]
- BEDNARIK, R. G. 2008c. The mythical Moderns. *Journal of World Prehistory* 21(2): 85–102. [RGB]
- BEDNARIK, R. G. 2011. *The human condition*. Springer, New York. [RGB] [VFS]
- BEDNARIK, R. G. and P. A. HELVENSTON in press. The nexus between neurodegeneration and advanced cognitive abilities. *Anthropos* 106(2). [PAH] [RGB]
- BIRD, R. and E. A. SMITH 2005. Signaling theory, strategic interaction, and symbolic capital. *Current Anthropology* 46: 221–248.
- BROWN, S. and E. DISSANAYAKE 2009. The arts are more than aesthetics: neuroaesthetics as narrow aesthetics. In M. Skov and O. Vartanian (eds), *Neuroaesthetics*, pp. 43–57. Baywood, Amityville, NY. [ED]
- BROWN, S., X. GAO, L. TISDELLE and M. LIOTTI in prep. Naturalizing aesthetics: Brain areas for aesthetic appraisal across sensory modalities.
- BUSS, D. M. 2009. How can evolutionary psychology successfully explain personality and individual differences? *Perspectives on Psychological Science* 4(4): 359–366. [VFS]
- BUSS, D. M. and H. GREILING 1999. Adaptive individual differences. *Journal of Personality* 67(2): 209–243. [VFS]
- CALDWELL, D. 2010a. Supernatural pregnancies. *Arts & Cultures*, pp. 52–75. Barbier-Mueller Museum, Geneva. [DC]
- CALDWELL, D. 2010b. The identification of the first Palaeolithic animal sculpture in the Ile-de-France: the Ségognole 3 bison and its ramifications. *Pre-acts of the IFRAO congress on Pleistocene art of the world*. [DC]
- CAMPBELL, A. and ROBBINS, L. 2009. Tsodilo Hill, Botswana. *Adoranten* 9: 34–48.
- CAVALLI-SFORZA, L. L. and M. W. FELDMAN 1973. Cultural vs. biological inheritance. *American Journal of Human Genetics* 25: 618–637. [RGB]
- CELA-CONDE, C. J., G. MARTY, F. MAESTU, T. ORTIZ, E. MUNAR,

- A. FERNANDEZ, M. ROCA, J. ROSELLO and F. QUESTNEY 2004. Activation of the prefrontal cortex in the human visual aesthetic perception. *Proceedings of the National Academy of Sciences* 101: 6321–6325. [BW]
- CHASE, P. G. 2010. *The emergence of culture: the evolution of a uniquely human way of life*. Springer, New York. [PAH]
- CHERNOFF, J. M. 1979. African rhythm and African sensibility: aesthetics and social action in African musical idioms. The University of Chicago Press, Chicago. [ED]
- CHEYNE, J. A. 1993. Signs of consciousness: speculations on the psychology of Paleolithic graphics. From <http://watarts.uwaterloo.ca/~acheyne/signcon.html>
- CHEYNE, J. A., L. MESCHINO and D. SMILEK 2009. Caricature and contrast in the Upper Palaeolithic: morphometric evidence from cave art. *Perception* 38: 100–108.
- COE, K. 2003. *The ancestress hypothesis: visual art as adaptation*. Rutgers University Press, New Brunswick, NJ.
- COOK, W. J. 1997. GM is getting looks. *US news World Rep* 122: 48–53.
- COSS, R. G. 1967. De nouveaux concepts esthétiques et le comportement du consommateur. *Design Industrie* 84: 84–85.
- COSS, R. G. 1990. All that glistens: water connotations in surface finishes. *Ecological Psychology* 2(4): 367–380. [ED]
- CRONIN, H. 1991. *The ant and the peacock*. Cambridge University Press, Cambridge.
- CZIKO, G. 1997. *Without miracles: universal selection theory and the second Darwinian revolution*. MIT Press, Cambridge, Mass. [AA]
- DALY, M. and M. WILSON 2001. Risk-taking, intrasexual competition, and homicide. *Nebraska Symposium on Motivation* 47: 1–36. [VFS]
- DARWIN, C. [1859]. *The origin of species*. 1928 reprint of 6th edn, Dent, London. [LD]
- DARWIN, C. 1871. *The descent of man and selection in relation to sex*. John Murray, London.
- DARWIN, C. [1871]. *The descent of man*. 1952 reprint, Encyclopaedia Britannica, University of Chicago. [LD]
- DARWIN, C. 2007. *The descent of man, and selection in relation to sex* (concise edition). Plume Book, New York. [AA]
- DAWKINS, R. 1982. *The extended phenotype: the long reach of the gene*. Oxford University Press, Oxford.
- DENNETT, D. 1995. *Darwin's dangerous idea: evolution and the meanings of life*. Penguin, London. [LD]
- DIAMOND, J. 2006. *The third chimpanzee*. Harper Perennial, New York.
- DICKIE, G. 1969. The myth of the aesthetic attitude. In J. Hospers (ed.), *Introductory readings in aesthetics*, pp. 28–45. Macmillan, London. [LD]
- DISSANAYAKE, E. 1988. *What is art for?* University of Washington Press, Seattle.
- DISSANAYAKE, E. 1992. *Homo aestheticus: where art comes from and why*. University of Washington Press, Seattle.
- DISSANAYAKE, E. 1995. *Homo aestheticus: where art comes from and why*. University of Washington Press, Seattle, WA. [PAH]
- DISSANAYAKE, E. 2000a. *Art and intimacy*. University of Washington Press, Seattle.
- DISSANAYAKE, E. 2000b. Antecedents of the temporal arts in early mother-infant interaction. In N. L. Wallin et al. (eds), *The origins of music*, pp. 389–410. MIT Press, Cambridge, MA. [AA]
- DISSANAYAKE, E. 2006. Ritual and ritualization: musical means of conveying and shaping emotion in humans and other animals. In S. Brown and U. Voglsten (eds), *Music and manipulation: on the social uses and social control of music*, pp. 31–56. Berghahn Books, Oxford and New York. [PAH]
- DISSANAYAKE, E. 2007. What art is and what art does: an overview of contemporary evolutionary hypotheses. In C. Martindale, P. Locher and V. M. Petrov (eds), *Evolutionary and neurocognitive approaches to aesthetics, creativity and the arts*, pp. 1–14. Baywood, Amityville, NY. [ED] [AA] [VFS]
- DISSANAYAKE, E. 2008. The arts after Darwin: does art have an origin and adaptive function? In K. Zijlman and W. van Damm (eds), *World art studies: exploring concepts and approaches*, pp. 241–263. Valiz, Amsterdam. [PAH]
- DISSANAYAKE, E. 2009. The artification hypothesis and its relevance to cognitive science, evolutionary aesthetics, and neuroaesthetics. *Cognitive Semiotics* (Special Issue on Aesthetic Cognition) 5: 148–173. [ED] [VFS]
- DISSANAYAKE, E. 2010. The deep structure of Pleistocene rock art: the 'artification hypothesis'. Pré-actes du congrès, IFRAO Ariège 2010, Pleistocene art of Europe, DVD, Lacombe, Tarascon-sur-Ariège.
- DURHAM, W. H. 1991. *Coevolution: genes, culture, and human diversity*. Stanford University Press, Stanford. [RGB]
- DUTTON, D. 2009a. *The art instinct*. Oxford University Press, Oxford.
- DUTTON, D. 2009b. *The art instinct: beauty, pleasure, and human evolution*. Bloomsbury Press, New York. [PAH]
- EDELMAN, G. M. 2006. *Second nature: brain science and human science*. Yale University Press, New Haven and London. [AA]
- EIBL-EIBESFELDT, I. 1989a. *Human ethology*. Aldine de Gruyter, New York.
- EIBL-EIBESFELDT, I. 1989b. The biological foundations of aesthetics. In I. Rentschler, B. Herzberger and D. Epstein (eds), *Beauty and the brain: biological aspects of aesthetics*, pp. 29–68. Birkhauser, Basel. [ED]
- ELFENBEIN, H. A. and N. AMBADY 2002. On the universality and cultural specificity of emotion recognition: a meta-analysis. *Psychological Bulletin* 128(2): 203–235. [VFS]
- ENQUIST, M. and A. ARAK 1993. Selection of exaggerated male traits by female aesthetic senses. *Nature* 361(4): 446–448.
- ENQUIST, M. and A. ARAK 1994. Symmetry, beauty and evolution. *Nature* 372(10): 169–172. [BW]
- FARRONI, T.; M. H. JOHNSON, E. MENON, L. ZULIAN, D. FARAGUNA and G. CSIBRA 2005. Newborns' preference for face-relevant stimuli: effects of contrast polarity. *Proceedings of National Academy of Sciences of the United States of America* 47: 17245–17250.
- FELDMAN, M. W. and L. L. CAVALLI-SFORZA 1989. On the theory of evolution under genetic and cultural transmission with application to the lactose absorption problem. In M. W. Feldman (ed.), *Mathematical evolutionary theory*, pp. 145–173. Princeton University Press, Princeton. [RGB]
- FONT, E. and P. CARAZO 2010. Animals in translation: why there is meaning (but probably no message) in animal communication. *Animal Behavior* 80(2): e1–e6.
- FUNCH, B. S. 1997. *The psychology of art appreciation*. Museum Tusulanum Press, Copenhagen.
- GANGESTAD, S. W. and J. A. SIMPSON 2000. The evolution of human mating: trade-offs and strategic pluralism. *Behavioral and Brain Sciences* 23: 573–587. [VFS]
- GAUTAM, M. 2001. Going the wild way. Homosexuality: its impact on creativity and inclination towards creative pursuits. *Creative Strategies* Fall 2001, pp 1–25. <http://www.rosenfels.org/nsc/Gautam.pdf> [AA]
- GEARY, D. C. 2002. Sexual selection and human life history. In R. V. Kail (org.), *Advances in child development and behaviour* 30: 41–101. Academic Press, San Diego, CA. [VFS]

- GOMBRICH, E. H. [1950]. *The story of art*. 1972 revised edn, Phaidon, London. [LD]
- GOMBRICH, E. H. 1962. *Art and illusion: a study in the psychology of pictorial representations*. Phaidon Press, London.
- GOMBRICH, E. H. 1978. *Meditations on a hobby horse, and other essays on the theory of art*. Phaidon, London. [BW]
- GOMBRICH, E. H. 1979. *The sense of order: a study in the psychology of decorative art*. Phaidon, Oxford. [BW]
- GOODWIN, F. K. and K. R. JAMISON 1990. *Manic depressive illness*. Oxford University Press, Oxford. [PAH]
- GOREN-INBAR, N. 1986. A figurine from the Acheulian site of Berekhat Ram. *Mi'Tekufat Ha'Even* 19: 7–12. [PAH]
- GOULD, S. J. 1980. *The panda's thumb: more reflections in natural history*. Norton, New York. [LD] [VFS]
- GOULD, S. J. 2002. *The structure of evolutionary theory*. Harvard University Press. [LD]
- GOULD, S. J. and E. S. VRBA 1982. Exaptation — a missing term in the science of form. *Paleobiology* 8(1): 4–15. [AA]
- GRAFEN, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144: 517–546.
- GRAMMER, K., B. FINK, A. P. MOLLER and R. THORNHILL 2003. Darwinian aesthetics: sexual selection and the biology of beauty. *Biological Review* 78: 385–407.
- GRAMMER, K. and R. THORNHILL 1994. Human facial attractiveness and sexual selection: the role of symmetry and averageness. *Journal of Comparative Psychology* 108: 233–242. [RGB]
- GRILL-SPECTOR, K., Z. KOURTZI and N. KANWISHER 2001. The lateral occipital complex and its role in object recognition. *Visual Research* 41: 1409–1422.
- GRINDE, B. 2000. A biological perspective on musical appreciation. *Nordic Journal of Music Therapy* 9(2): 18–27.
- GURVEN, M., W. ALLEN-ARAVE, K. HILL and M. HURTADO 2000. It's a wonderful life: signaling generosity among the Ache of Paraguay. *Evolution and Human Behavior* 21: 263–282.
- GUTHRIE, R. D. 2005. *The nature of Paleolithic art*. University of Chicago Press, Chicago. [BW] [AA]
- HADINGHAM, E. 1979. *Secrets of the Ice Age: the world of cave artists*. Walker, New York. [PAH]
- HAMMERMEISTER, K. 2002. *The German aesthetic tradition*. Cambridge University Press, Cambridge. [LD]
- HELVENSTON, P. A. and R. G. BEDNARIK in press. Evolutionary origins of brain disorders in *Homo sapiens sapiens*. *NOVA Brain Research Journal*. [PAH]
- HELVENSTON, P. A. and D. HODGSON 2010. The neuropsychology of 'animism': implications for understanding rock art. *Rock Art Research* 27: 61–94.
- HENSHILWOOD, C. S., F. D'ERRICO, R. YATES, Z. JACOBS and C. TRIBOLO 2002. Emergence of modern human behavior: Middle Stone Age engravings from South Africa. *Science* 295: 1278–1280. [PAH]
- HENSHILWOOD, C. S., F. D'ERRICO, M. VANHAEREN, K. VAN NIEKERK and Z. JACOBS 2004. Middle Stone Age shell beads from South Africa. *Science* 304: 404. [PAH]
- HEYD, T. and J. CLEGG 2004. Re-thinking aesthetics and rock art. Paper presented to the IFRAO Congress, Agra.
- HEYD, T. and J. CLEGG (eds) 2005. *Aesthetics and rock art*. Ashgate Publishing, Hampshire.
- HIMMELHEBER, H. 1993. *Eskimo artists: fieldwork in Alaska, June 1936 until April 1937*. Translated by D. G. Gunderson and author. University of Alaska Press, Fairbanks. (Originally published as *Eskimo-Künstler: Teilergebnis einer ethnographischen Expedition in Alaska von Juni 1936–April 1937*. Strecker & Schröder, Stuttgart, 1938). [ED]
- HODGSON, D. 2000. Art, perception and information processing: an evolutionary perspective. *Rock Art Research* 17: 3–34. [ED]
- HODGSON, D. 2009a. Evolution of the visual cortex and the emergence of symmetry in the Acheulian techno-complex. *Comptes Rendus Palevol* 8: 93–97. [BW]
- HODGSON, D. 2009b. Symmetry and humans: reply to Mithen's 'sexy handaxe theory'. *Antiquity* 83(319): 195–198. [BW]
- HORTON, R. 1965. *Kalabari sculpture*. Nigerian National Press for Department of Antiquities, Apapa, Lagos. [ED]
- HOWLEY, A. 2010. World's oldest optical illusion found? NatGeo News Watch. <http://blogs.nationalgeographic.com/blogs/news/chiefteditor/2010/12/worlds-oldest-optical-illusion.html> [DC]
- HUIZINGA, J. 1956. *Homo ludens: a study in the play-element in culture*. Beacon Press, Boston. [AA]
- IZARD, C. E. 1994. Innate and universal facial expression: evidence from development and cross-cultural research. *Psychological Bulletin* 115(2): 288–299. [VFS]
- JABLONKA, E. and M. LAMB 2005. *Evolution in four dimensions: genetic, epigenetic, behavioral, and symbolic variation in the history of life*. MIT Press, Cambridge, MA. [PAH]
- JABLONSKI, N. G. 2004. The evolution of human skin and skin color. *Annual Review of Anthropology* 33: 585–623. [AA]
- JACOBSON, T., R. I. SCHUBOLTZ, L. HOFEL and D. Y. CRAMON 2006. Brain correlates of aesthetic judgement of beauty. *Neuroimage* 29: 276–285. [BW]
- JONES, D. M. 1995. Sexual selection, physical attractiveness and facial neoteny: cross-cultural evidence and implications. *Current Anthropology* 36(5): 723–748. [RGB]
- JONES, D. M. 1996. An evolutionary perspective on physical attractiveness. *Evolutionary Anthropology* 5(3): 97–109. [RGB]
- KANAZAWA, S. 2000. Scientific discoveries as cultural displays: a further test of Miller's courtship model. *Evolution and Human Behavior* 21: 317–321. [VFS]
- KANT, I. [1790]. *Critique of judgment*. Transl. J. H. Bernard, 1951 reprint, Hafner, New York. [LD]
- KAWABATA, H. and S. ZEKI 2004. Neural correlates of beauty. *Journal of Neurophysiology* 91: 1699–1705. [BW]
- KOHN, M. and S. MITHEN 1999. Handaxes: products of sexual selection? *Antiquity* 73: 518–526. [BW]
- KORTLAND, A. 1962. Chimpanzees in the wild. *Scientific American* 206(5): 128–138. [PAH]
- KRINGELBACH, M. L. 2009. *The pleasure center: trust your animal instinct*. Oxford University Press, New York. [AA]
- LALAND, K. N. 1994. Sexual selection with a culturally transmitted mating preference. *Theoretical Population Biology* 45: 1–15. [RGB]
- LALAND, K., J. ODLING-SMEE and M. W. FELDMAN 2000. Niche construction, biological evolution and cultural change. *Behavioral and Brain Sciences* 23: 131–175. [PAH]
- LALAND, K., J. ODLING-SMEE and S. MYLES 2010. How culture shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics* 11: 137–148. [PAH]
- LANGE, B. P. 2010. Sexual selection for literary displays. In L. Sugiyama and M. S. Sugiyama (orgs), *Annals of the 22nd Annual Meeting of the Human Behavior and Evolution Society*, p. 65. University of Oregon, Eugene. [VFS]
- LANGLOIS, J. H., L. A. ROGGMAN and L. A. REISER-DANNER 1990. Infant's differential social responses to attractive and unattractive faces. *Developmental Psychology* 26: 153–159.
- LASHERAS, J. A. 2009. The cave of Altamira: 22,000 years of history. *Adoranten* 9: 5–33.
- LOTEM, A., M. A. FISHMAN and L. STONE 2002. From reciprocity to unconditional altruism through signaling benefits. *Proceedings of the Royal Society of London, Series B*:

- Biological Sciences 270: 199–205.
- LOW, B. S. 1998. The evolution of human life histories. In C. Crawford and D. L. Krebs (orgs), *Handbook of Evolutionary Psychology*, pp. 131–162. Lawrence Erlbaum, Mahwah, NJ. [VFS]
- LOYAU, A., M. SAINT-JALME, C. CAGNIANT and G. SORCI 2005. Multiple sexual advertisements honestly reflect health status in peacocks (*Pavo cristatus*). *Behavioral Ecology and Sociobiology* 58: 552–557.
- MACANDREW, F. T. 2002. New evolutionary perspective on altruism: multilevel-selection and costly-signaling theories. *Current Directions in Psychological Science* 11: 79–82.
- MCCCLUSKY, P. 2002. The fetish and the imagination of Europe; sacred medicines of the Kongo. *Art from Africa: long steps never broke a back*, pp. 143–169. Seattle Art Museum, Seattle. [DC]
- MCDONALD, J. 2005. Archaic faces to headdresses: the changing role of rock art across the arid zone. In P. M. Veth, M. A. Smith and P. Hiscock (eds), *Desert peoples: archaeological perspectives*, pp. 116–140. Wiley-Blackwell, Melbourne.
- MALOTKI, E. and D. E. WEAVER 2001. *Stone chisel and yucca brush: Colorado Plateau rock art*. Kiva Publishing, Walnut Creek, CA.
- MARSHACK, A. A. 1997. The Berekhat Ram figurine: a late Acheulian carving from the Middle East. *Antiquity* 71: 327–227. [PAH]
- MAYR, E. 2004. *What makes biology unique? Considerations on the autonomy of a scientific discipline*. Cambridge University Press, Cambridge.
- MESOUDI, A., A. WHITEN and K. N. LALAND 2006. Towards a unified science of cultural evolution. *Behavioral and Brain Sciences* 29: 329–383. [PAH]
- MICHAELIS, D. 2008. *Schulz and Peanuts: a biography*. Harper Perennial, New York. [AA]
- MILLER, G. F. 1999. Sexual selection for cultural displays. In R. Dunbar, C. Knight, and C. Power (eds), *The evolution of culture*, pp. 71–91. Rutgers University Press, New Brunswick. [VFS]
- MILLER, G. F. 2000a. How to keep our meta-theories adaptive: beyond Cosmides, Tooby, and Lakatos. *Psychological Inquiry* 11: 42–46.
- MILLER, G. F. 2000b. *The mating mind: how sexual choice shaped the evolution of human nature*. Doubleday, New York.
- MILLER, G. F. 2001. Aesthetic fitness: how sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria. *Bulletin of Psychology and the Arts* 2(1): 20–25. Special issue on Evolution, creativity and aesthetics.
- MILLER, G. F. 2003. Fear of fitness indicators: how to deal with our ideological anxieties about the role of sexual selection in the origins of human culture. In *Being human: proceedings of a conference sponsored by the Royal Society of New Zealand*, 65–79. Royal Society of New Zealand, Miscellaneous series 63, Wellington.
- MITHEN, S. 2003. Handaxes: the first aesthetic artefacts. In E. Voland (ed.), *Evolutionary aesthetics*, pp. 261–275. Springer-Verlag, Berlin. [BW]
- MØLLER, A. P. and M. PETRIE 2002. Condition dependence, multiple sexual signals, and immunocompetence in peacocks. *Behavioral Ecology* 13: 248–253
- MONZON, S. 1980. Des rapports entre les signes et les représentations anthropomorphes dans les peintures rupestres du Brésil. *Journal de la Société des Américanistes* 67: 125–140.
- MORRIS, D. 1962. *The biology of art*. Methuen, London. [PAH]
- MORRIS, D. 1998. Foreword. *The Cambridge illustrated history of prehistoric art*, University Press, Cambridge.
- NETTLE, D. and H. CLEGG 2005. Schizotypy, creativity and mating success in humans. *Proceedings of the Royal Society – Biological Sciences* 273: 611–615. [PAH] [AA]
- ODLING-SMEE, F. J., K. N. LALAND and M. W. FELDMAN 2003. *Niche construction: the neglected process in evolution*. Princeton University Press, Princeton, NJ. [PAH]
- O'HANLON, M. 1989. *Reading the skin: adornment, display, and society among the Wahgi*. British Museum Publications, London. [ED]
- OYAMA, S. 2000 *Evolution's eye: a systems view of the biology-culture divide*. Duke University Press, Durham, NC. [PAH]
- OYAMA, S., P. E. GRIFFITHS and R. D. GRAY 2001. *Cycles of contingency: developmental systems and evolution*. MIT Press, Cambridge, MA. [PAH]
- PALMER, S. E., J. S. GARDNER and T. D. WICKENS 2008. Aesthetic issues in spatial composition: effects of position and direction on framing single objects. *Spatial Vision* 21(3–5): 421–449.
- PARKER, S. T. and K. E. JAFFE 2008. *Darwin's legacy: scenarios in human evolution*. Altamira Press, New York. [AA]
- PAUL, G. 1988. Philosophical theories of beauty and scientific research on the brain. In I. Rentschler, B. Herzberger and D. Epstein (eds), *Beauty and the brain: biological aspects of aesthetics*, pp. 15–27. Birkhauser, Basel. [BW]
- PESSIS, A. and N. GUIDON 2007. Serra da Capivara National Park, Brazil: cultural heritage and society. *World Archaeology* 39(3): 406–416.
- PINKER, S. 2002. *The blank slate: the modern denial of human nature*. Penguin Books, New York.
- POWER, C. 1999. 'Beauty magic': the origins of art. In R. Dunbar, C. Knight and C. Power (eds), *The evolution of culture*, pp. 92–112. Edinburgh University Press, Edinburgh.
- RAMACHANDRAN, V. S. 2003. *The emerging mind*. Profile Books, London. [LD]
- RAMACHANDRAN, V. S. and W. HIRSTEIN 1999. The science of art: a neurological theory of aesthetic experience. *Journal of Consciousness Studies* 6(6–7): 15–51.
- RENDALL, D.; M. J. OWREN and M. J. RYAN 2009. What do animal signals mean? *Animal Behaviour* 78: 233–240.
- RIDLEY, M. 1993. *The red queen: sex and the evolution of human nature*. HarperCollins, New York.
- SAHLINS, M. 1978. *The use and abuse of biology: an anthropological critique of sociobiology*. The University of Michigan Press, Ann Arbor. [AA]
- SAPIR, E. 1929. The status of linguistics as science. *Language* 5: 207–214. [RGB]
- SAUVET, G. and A. WŁODARCZYK, 2008. Towards a formal grammar of the European Palaeolithic cave art. *Rock Art Research* 25: 165–172.
- SCHMITT, D. P. and J. J. PILCHER 2004. Evaluating evidence of psychological adaptation. How do we know one when we see one? *Psychological Science* 15(10): 643–649.
- SCHMITT, D. P. et al. 2005. Sociosexuality from Argentina to Zimbabwe: a 48-nation study of sex, culture and strategies of human mating. *Behavioral and Brain Sciences* 28: 247–275. [VFS]
- SHACKELFORD, T. K. and R. J. LARSEN 1997. Facial asymmetry as an indicator of psychological, emotional, and physiological distress. *Journal of Personality and Social Psychology* 72(1): 456–466. [RGB]
- SHANER, A. G. MILLER and J. MINTZ 2008. Mental disorder as catastrophic failures of mating intelligence. In G. Geher and G. Miller (eds), *Mating intelligence*, pp. 193–215. Law-

- rence Erlbaum Associates, New York. [AA]
- SILK, J. B. 2007. Social component of fitness in primate groups. *Science* 317: 1347–1351. [PAH]
- SKAMEL, U. 2003. Beauty and sex appeal: sexual selection of aesthetic preferences. In E. Voland and K. Grammer (org.), *Evolutionary aesthetics*, pp. 173–200. Springer, Berlin.
- SMITH, E. A. and R. L. BIRD 2000. Turtle hunting and tombstone opening: public generosity as costly signaling. *Evolution and Human Behavior* 21: 245–261.
- SOSIS, R. 2000. Costly signaling and torch fishing on Ifaluk Atoll. *Evolution and Human Behavior* 21: 223–244.
- SOUZA, R. 2004. Is art an adaptation? Prospects for an evolutionary perspective on aesthetic emotions. *Journal of Aesthetics and Art Criticism* 62(2): 109–118.
- STOTT, M. A. 1975. *Bella Coola ceremony and art*. National Museums of Canada, Ottawa. [ED]
- SUGIYAMA, L. S. and M. SCALISE SUGIYAMA 2003. Social roles, prestige, and health risk: social niche specialization as a risk buffering strategy. *Human Nature* 14(2): 165–190. [ED]
- TAÇON, P. S. C., L. GANG, Y. DECONG, S. K. MAY, L. HONG, M. AUBERT, J. XUEPING, D. CURNOE and A. I. R. HERRIES 2010. Naturalism, nature and questions of style in Jinsha River rock art, northwest Yunnan, China. *Cambridge Archaeological Journal* 20: 67–86.
- TAMBIAH, S. J. 1979. A performative approach to ritual. *Proceedings of the British Academy, London* 65: 113–169. University Press, Oxford. [ED]
- TANSEM, K. and H. JOHANSEN 2008. The World Heritage Rock Art in Alta. *Adoranten* 9: 65–84.
- THORNHILL, R. 2003. Darwinian aesthetics informs traditional aesthetics. In E. Voland and K. Grammer (eds), *Evolutionary aesthetics*, pp. 9–38. Springer, Berlin.
- TINBERGEN, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20: 410–433. (Reprinted in J. J. Bolhuis and S. Verhulst (eds), 2009, *Timbergen's legacy: function and mechanism in behavioral biology*, Cambridge University Press, Cambridge.)
- TOOBY, J. and L. COSMIDES 1989. The innate versus the manifest: how universal does universal have to be? *Behavioral and Brain Sciences* 12(1): 36–37. [VFS]
- VARTANIAN, O. and V. GOE 2004. Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport* 15(5): 893–897. [BW]
- VELDEN, M. 2010. *Biologism: the consequence of an illusion*. V & T Unipress, Goettingen. [AA]
- VILLENEUVE, S. N. 2008. Looking at caves from the bottom-up: a visual and contextual analysis of four Paleolithic painted caves in southwest France (Dordogne). Unpubl. thesis, University of Victoria. https://dspace.library.uvic.ca:8443/dspace/bitstream/1828/2875/1/Vileneuve_S_MA.pdf
- VOLAND, E. 2003. Aesthetic preferences in the world of artifacts. Adaptation for the evaluation of honest signals? In E. Voland and K. Grammer (org.) *Evolutionary aesthetics*, pp. 239–260. Springer, Berlin.
- VOLAND, E. and K. GRAMMER 2003. From Darwin's thoughts on the sense of beauty to evolutionary aesthetics. In E. Voland and K. Grammer (org.), *Evolutionary aesthetics*, pp. 1–8. Springer, Berlin.
- WALLACE, H. D. 2008. The petroglyphs of Atlatl Ridge, Tortolita Mountains, Pima County, Arizona. In D. L. Swartz (ed.), *Life in the foothills: archaeological investigations in the Tortolita Mountains of southern Arizona*, pp. 159–231. Anthropological Papers 46, Center for Desert Archaeology, Tucson, Arizona. [ED]
- WATSON, B. 2008. Oodles of doodles? Doodling behaviour and its implications for understanding palaeoarts. *Rock Art Research* 25: 35–60.
- WATSON, B. 2009. Universal visions: neuroscience and recurrent characteristics of world palaeoart. Unpubl. PhD thesis, Centre for Classics and Archaeology, University of Melbourne. [BW]
- WATSON, B. 2010. The neuropsychology of animism and implied motion in rock art. Comment on P. A. Helvenston and D. Hodgson, 'The neuropsychology of "animism": implications for understanding rock art'. *Rock Art Research* 17: 79–80.
- WATSON, B. 2011. The eyes have it: human perception and anthropomorphic faces in world rock art. *Antiquity* 85(327): 87–98. [BW]
- WATSON, B. in prep. The body and the brain: neuroscience and the representation of anthropomorphs in palaeoart. *Rock Art Research*. [BW]
- WERNER, G. M. and P. M. TODD 1997. Too many love songs: sexual selection and the evolution of communication. In P. Husbands and I. Harvey (eds), *ECAL97*, pp. 434–443. MIT Press, Cambridge.
- WEST, S. A., A. GARDNER and A. S. GRIFFIN 2008. Kinship and social behavior. In C. Crawford and D. Krebs (eds), *Foundations of evolutionary psychology*, pp. 91–114. Taylor & Francis, New York, NY. [VFS]
- WHITLEY, D. S. (ed.) 2001. *Handbook of rock art research*. AltaMira Press, Walnut Creek, CA.
- WILLIAMS, G. C. 1992. *Natural selection: domains, levels, and challenges*. Oxford University Press, New York.
- WILSON, E. O. 1984. *Biophilia*. Harvard University Press, Cambridge, MA. [PAH]
- WINTERHALDER, B. and E. A. SMITH 2000. Analyzing adaptive strategies: human behavioral ecology at twenty-five. *Evolutionary Anthropology* 9(2): 51–72. [VFS]
- ZAHAVI, A. and A. ZAHAVI 1997. *The handicap principle: a missing piece of Darwin's puzzle*. Oxford University Press, New York.
- ZEKI, S. 1999. *Inner vision: an exploration of art and the brain*. Oxford University Press, Oxford. [BW]