

# The Evolution of Aesthetics: a Review of Models

Julien P. Renoult

*Institute of Arts Creations Theories & Aesthetics, CNRS-University Paris 1 Panthéon-Sorbonne, 47 r. des bergers, 75015, Paris, France*

## Abstract

The evolution of aesthetics has become an increasingly popular topic over the last few years, both for evolutionary biologists and for scholars from other disciplines who want to broaden the historical perspective of their findings. Different models have been proposed to explain evolution of aesthetics, all inspired from research in sexual selection. In this chapter, I review three of these models: beauty as an indicator of quality, Fisher's model of aesthetic coevolution, and the exploitation of efficient information processing. I argue that only the last model can simultaneously explain the ubiquity and universality of aesthetic experiences, and the diversity and extravagancy of beautiful stimuli. The model fits both to empirical results from psychology and image statistics showing that beautiful stimuli are efficiently processed by perceptual and cognitive systems, and to neurophysiological evidences supporting the concept "disinterestedness" in philosophy of aesthetics. The exploitation of efficient processing uniquely offers a workable model for evolutionary biology that further articulates with concepts and results from other aesthetic sciences.

## X.1. Introduction

Aesthetics is a vibrant topic, one of those that enthral societies and equally enliven researchers from all fields. For more than a century, research on aesthetics has become a real science, with a methodology and accumulative evolution of knowledge similar to those classically observed in biology or physics. Works in cognitive sciences in particular have much contributed to unravel the proximate mechanisms underlying the aesthetic experience<sup>1</sup>. As usual, however, the haecceity of a biological thing or phenomenon is best understood when framing its study with an evolutionary perspective. This chapter will review three models that evolutionary biologists have proposed to explain aesthetic evolution.

In evolutionary biology, little attention has been paid to the definition of aesthetics and beauty, either treated as synonymous with preference, or with attractiveness, or not defined at all. As argued at the end of this contribution, this casualness may have hampered progress in our understanding of aesthetic evolution. For present purposes, and to stick with the referred literature, I will define aesthetics very roughly as the feeling experienced by individuals facing a stimulus and that could

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<sup>1</sup> Throughout this review, *beauty* will refer to "the inherent property of a (visual) stimulus" and *aesthetics* to "the subjective experience elicited by beautiful stimuli" (Redies et al. 2015). *Aesthetic valuation* will describe the mind process of placing a stimulus on a scale from ugly to beautiful. *Aesthetic appeal* is the attractiveness of a stimulus due to its beauty, and *aesthetic preference* the aesthetic appeal of a stimulus relative to that of other stimuli.

be talked out with a “wouaouh!!”. Although not scientifically sound, this definition allows readers who already experienced aesthetics to grasp the type of feeling that is discussed in this review (see also Palmer et al. 2013). Thinking aesthetics in terms of “wouaouh!!” further allows listing basic criteria that could characterize aesthetics and beauty without too much contentiousness. First, aesthetics seems ubiquitous. We enjoy staring at very different kind of stimuli in a variety of contexts, including art exhibitions, starlight, potential mates, or a she-cat licking her kitten. Second, focusing on a specific kind of stimuli and contexts, beautiful stimuli seems highly diversified. There are for instance plenty of artworks that have the power to delight us, and even for one particular type of artworks, say abstract paintings, aesthetic possibilities seems infinite. Third, many beautiful stimuli appear extravagant. This is particularly true for organic communicative stimuli. Extravagancy may not be a necessary condition to beautifulness, but it certainly contributes to make us appreciating the abundance of forms and colours in birds of paradise (Paradisaeidae), the frantic dance of Blue butterflies (Polyommatainae), the loud and penetrating call of the indri lemur (*Indri indri*) or the immoderate excessiveness of the labellum of the Lizard orchid (*Himantoglossum hircinum*). Last, despite this huge diversity of beautiful stimuli and aesthetic experiences, people seem alike bewitched by the same stimuli. Sunsets, for example, wow people from over the world. Certainly this last point will not be taken for granted by everyone at this stage, but it will be thoroughly discussed in the following. These four criteria will be used as a guideline to evaluate the ability of the different models to provide an encompassing explanation to aesthetic evolution.

The first model discussed is the indicator of quality, which is the most notorious model of aesthetic evolution, although probably not the best understood. I will then review a model rooting far in the first half of the twentieth century, but which has been only recently valued as a primary model of aesthetic evolution: Fisher’s runaway. Last, I will conclude with studies supporting that aesthetics is a by-product of perceptual and cognitive adaptations to efficiently process information.

## **X.2. Beauty: an indicator of quality**

The evolution of aesthetics has been mostly investigated by evolutionary psychologists. The goal of evolutionary psychology is to understand the design of human mind using the principles of evolutionary biology (Barkow et al. 1995). In fact, evolutionary psychology has focused so much on adaptation as the main determinant of evolution that one can fairly qualify this field of research “an adaptationist approach to evolution of the human mind”. For evolutionary psychologists, perception, emotion, cognition and the actions resulting from these mind processes all are adaptations designed by natural and sexual selection having allowed people to survive and reproduce during the evolutionary history of our species. Aesthetic valuation is a product of the mind and thus a manifestation of these adaptations (Cosmides and Tooby 1987). By extension, aesthetic valuation itself has been considered an adaptation. Aesthetic valuation is a psychological manifestation that, consciously or not, evaluates the benefit of the environment (including both its inanimate and living constituents) in terms of survival and reproduction (Thornhill 2003). We see beauty in what or who increases our

likelihood to survive and to produce offspring, and ugliness in what or who is a bad omen. Beauty is thus a stimulus indicating the quality of what is perceived<sup>2</sup>.

According to the model of quality indicator, those forebears that were lucky to have a mind manifestation for appraising the quality of perceived objects and organisms survived longer, reproduced more, and thus transmitted this (originally fortuitous) ability more widely to next generations. This adaptationist model assumes that aesthetic valuation is determined genetically, and that aesthetic preferences are universal or at least shared between individuals or populations proportionally to their genetic similarity. In the following, I review some of the studies on the quality indicator model of aesthetic evolution that dealt with two types of stimuli: landscapes and the face of potential mates.

### **X.2.1. Landscapes**

The quality indicator model of aesthetic evolution proposes that our ancestors' minds have been selected to find landscapes beautiful when they were safe and plenty of resources. According to the so-called Savannah hypothesis, we have an innate preference for landscapes reminiscent of the savannah biome in which our African ancestors evolved (Orians and Heerwagen 1992). Accordingly, Balling and Falk (1982) found that American children expressed a significant preference for pictures of savannah rather than of other natural biomes. However, other studies revealed patterns that can be hardly explained by the Savannah hypothesis. In one study, Coeterier (1996) found preferences for landscapes with traces of human control. In another study, Han (2007) was not able to replicate Balling and Falk's results when explicitly asking subjects to evaluate scenic beauty (in the original study, reference to beauty was only implicit). In their study, the authors found the greatest aesthetic merit to coniferous and tundra biomes. More importantly, the basic assumption that our ancestors' minds should have adapted mainly to savannah biotopes does not fit archaeological evidences that during the last hundred thousand years of its evolution, our species experienced important climatic variations, shifting cyclically from temperate to tropical conditions. It thus seems unsupported that landscape aesthetics is an adaptation that evolved to evaluate the potential quality of one specific biome.

Studies on landscape aesthetics nevertheless evidenced several seemingly robust and generalizable patterns of preference (Ruso et al. 2003). First, we have an overall preference for natural over artificial landscapes (Kaplan and Kaplan 1989). Naturality is well known by urban planners to increase the aesthetic appeal of cities. Our propensity to grow tropical ferns indoor and to sow flowered lawn may reflect a deeply-rooted pleasure of inhabiting fertile land. In one study, tree density, tree placement and level of grass maintenance were manipulated on images of neighbourhood outdoor space that were shown to one hundred American inner-city residents living adjacent to that space (Kuo et al. 1998). Preferences went for densely wooded space independent of tree placement, which can be interpreted as cueing high land fertility. Second, we like safe landscapes. Safe landscapes are those we can control: we enjoy nature, but not complete wildness. In the same study, residents preferred well maintained over tall grass; and when residents were asked to score the expected safety of space in addition to their preference, the two scores were highly correlated. The importance of safety is further

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<sup>2</sup> In aesthetics, the expression "quality indicator" originally comes from research in sexual selection and refers to the quality of potential mates. Here, "quality" should be understood in the wide sense and can include quantitative aspects of the valued stimulus.

supported by several studies showing that we tend to prefer landscapes that can be monitored easily from a sheltered viewpoint (e.g., Appleton 1975). Third, landscape should contain water. Indeed, adding water dramatically increases the aesthetic appeal of landscapes (Ulrich 1981). In sum, there is reasonably large body of evidence that the preferred landscapes are those that are expected to provide refuge and resources, and thus facilitate survival and reproduction.

### **X.2.2. Faces**

According to the quality indicator model, our ancestors' minds have been selected to see beauty in good-quality people who can afford either direct benefit by providing resources or safety, or indirect benefit by transmitting good genes to offspring. In evolutionary psychology, and more generally in research on sexual selection in humans and animals, the model of quality indicator is the most popular model explaining why individuals tend to share the same preferences for sexual partners.

There is indeed a shared, universal component to face preferences. New-borns presented with face pictures spent a longer time gazing at faces that have been rated as attractive by adults, independently of the gender, ethnical origin (white versus black people) and age (infant versus adult) of the displayed faces (Langlois et al. 1991). It is assumed that, in humans at least, face preference is congenital and is reshaped during postnatal development to integrate individual experience and cultural standards. Nevertheless, a number of cross-cultural studies have shown that adults continue to share face preferences (Jones and Hill 1993; Zebrowitz et al. 1993; Zebrowitz et al. 2012), which suggests a genetic influence in the determination of this preference (Jones and Hill 1993).

Three facial attributes in particular seem to drive commonalities in face preference in humans (for a review, see Rhodes 2006)). The first one is symmetry. Preference for symmetrical faces has been found for both men's and women's faces (Grammer and Thornhill 1994), from different cultures and in cross-cultural experiments (Pisanski and Feinberg 2013). The second attribute that seems to drive commonalities in face preference is sexual dimorphism. Heterosexual men over the world are attracted by feminine women (Buss 1989). Women similarly tend to find masculine men more attractive, even though the effect is weaker than for feminine women (Rhodes 2006). The third facial attribute is averageness. Early evidence that an average face is appealing came from studies using computer-generated averaged composites of faces (Langlois and Roggman 1990). However, because blending makes averaged face looking more symmetrical and smoother, it was soon thought that these attributes, not averageness per se, were driving attractiveness. Further studies therefore replicated analyses while controlling for symmetry and smoothness, and confirmed previous findings (Rhodes et al. 1999). In addition, preference for average faces has been documented by studies on natural, non-manipulated faces (e.g., Light et al. 1981), and in one meta-analysis (Rhodes 2006).

The model of quality indicator supposes that we evolved to find averaged, sexually dimorphic and symmetrical faces beautiful because they cue beneficial mates. The link between symmetry and mate quality in particular has been the focus of a wealth of studies over the last three decades. Several authors proposed that symmetry reflects developmental stability, which depends on the genetic background and on external factors such as parasite load, nutrition, pollution (Møller 1992; Palmer and Strobeck 1986; Parsons 1990). Yet both the link between degree of symmetry and

developmental stability, and between developmental stability and mate quality seem more complex and idiosyncratic than previously thought (Dongen 2006; Polak et al. 2003). Most likely, symmetry is related to quality in some animals and for certain traits, but it is not for some others. Regarding human face specifically, one study showed that perceived health cancelled the effect of both symmetry and averageness in a statistical model explaining variation in attractive faces (Rhodes et al. 2007). This study supports the idea that the appeal of symmetric and averaged faces is largely due to their healthy appearance. Furthermore, genetic diversity within the major histocompatibility complex (MHC), which are proteins coding for immune response, positively predicted male attractiveness, with face averageness mediating the relationship (Lie et al. 2008). The relationship between health or genetic quality, and masculinity in men or femininity in women, is not as strongly supported (Rhodes 2006). However, men with higher levels of circulating testosterone, that is, stronger men that are more likely to provide direct benefits, are rated more masculine (Penton-Voak and Chen 2004), and women with higher levels of circulating oestrogen, that is, more fertile women, are rated more feminine (Law-Smith et al. 2006). Overall, the huge literature on face preference made convincing the hypothesis that attractive face partly indicates good-quality mates.

### **X.2.3. Cues, indices and honest signalling**

Landscapes and sexual partners both vary in how good they are to the perceiver. Landscapes with fertile lands, refuges, viewpoints and water are preferred because they are expected to be beneficial, and so are fertile and healthy women, and strong and healthy men. There is nevertheless a fundamental difference between landscapes and sexual partners. Being a biological organism the latter but not the former can evolve autonomously in response to selection by the beholder. Naturally, the quality of a landscape may change with time due to the action of humans or of any other ecosystem engineers, but a landscape cannot evolve autonomously. This means that a landscape will never evolve *signals*, which are adaptations influencing the behaviour of other organisms, and which evolved specifically because of that effect (Stevens 2013). The appraisal of landscape quality will always rely on cues, and on cues only, which are incidental sources of information (Stevens 2013). In contrast to signals, cue for example could never evolve a strategy that lures the beholder by purposely advertising a false level of quality.

A strong correlation between signals and quality characterises honest signalling. It is generally assumed that a communication system needs to be reliable on average to maintain over time. Indicating quality is always costly: sexual displays, gametes, but also flower nectar, fruit pulp or amphibian toxins all need energy to be produced. If the strategy of signalling these “quality” without effectively affording them were as efficient as honest signalling, it would spread and become the dominant strategy, eventually making the whole communication system unreliable and useless<sup>3</sup>.

A contentious question in evolutionary biology is how the correlation between signals and quality is achieved. The most frequently cited mechanism is the “handicap principle” (Zahavi 1975; Zahavi and Zahavi 1997). All textbooks in psychology, evolutionary aesthetics and neuroaesthetics I could read cite this mechanism, and most of them only cite this one. In short, the handicap principle proposes that honest signals

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<sup>3</sup> Naturally, deceptive signalling does exist, and the system can maintain with traces of unreliability if the cost of cheating is low, explaining for example why women continue to put makeup on and men to wear epaulets.

are maintained because they incur extra-costs that only truly good-quality individuals can bear. A classical example is the peacock tail. According to the handicap principle, the long tail of peacocks signals mate quality to peahens, and honesty is maintained because only those males that are in truly good health state can afford wasting energy or handicapping themselves (for example for fighting against rivals or escaping predators) by producing such long tails.

The theoretical conditions that make the handicap principle operative are quite restrictive, and several authors expressed concern that the mechanism has been abusively proposed to explain the maintenance of signal honesty (Számado 2011), in particular in the sociological and psychological literature (Grose 2011). It should be clear that the handicap principle relies on the existence of variation in the *extra-cost* of signal production, that this cost should be differentially higher for the lower quality individuals, and that the variation is correlated with heritable genetic variation in quality. Simply arguing, for instance, that making art is costly is far from being sufficient to fuel the idea that art is a handicapping sexual signal. As it turned out, very few if no one studies in evolutionary biology succeeded in collecting all the empirical evidences necessary to unambiguously favour the handicap principle over alternative mechanisms, to a point that several authors doubt that the handicap principle is relevant to organic evolution (Számado 2011; Getty 2006; Cotton et al. 2004).

Alternative mechanisms to explain the maintenance of reliable communication are numerous (Schaefer and Ruxton 2015). The most obvious one concerns signals that are reliable because they physically cannot be produced by low-quality individuals. Such signals are termed *indices* (Maynard-Smith and Harper 1995). An example of index is loud call, which is preferred by females in several animal species. Because call loudness is determined by the size of the sounding board, call loudness is an honest indicator of caller's vigour independently of the cost of calling (Stevens 2013). Another mechanism is based on public information, where cheaters are avoided because they have been previously observed cheating when interacting with a third party, or when the third party directly communicates about his bad experience (Danchin et al. 2004). Yet another mechanism relies on learning from past experience, which typically occurs in communication systems based on repeated, small-effect interactions (Schaefer and Ruxton 2015). For example, you may lose a few dollars going to the movie theatre to watch *Dude, Where's my car?* but it is unlikely you go again to watch another movie by Danny Leiner.

What about faces? It has been often suggested that feminine and masculine facial traits are honest indicators of positive quality because they indicate levels of circulating hormones during growth, which metabolisms are costly (Thornhill and Grammer 1999). Indeed, high level of oestrogen promotes certain hereditary diseases (Liang and Shang 2013) and high level of testosterone lowers immunocompetence (Folstad and Karter 1992). However, oestrogen and testosterone also and firstly have several beneficial effects, on follicle and sperm production, muscle development and strength, bone density, to name just a few (Burrows 2013). Thus, rather than signalling handicapping level of hormones, it seems more rational to interpret sexual dimorphic traits as (inevitably) honest cues of strength and fertility (see also Skamel 2003).

In sum, the quality indicator model of aesthetic evolution assumes that aesthetics valuation has evolved through the course of human's evolution to appraise the qualities of its environment in terms of survival and reproduction. The model seems to correctly explain which landscapes and human's faces people across cultures agree to prefer. It

could similarly explain preferences for many other items if these can be related to our vital needs. For example, according to this model we would find roe deers and strawberries aesthetically pleasing because they afford proteins and sugar, respectively, bird songs because they cue productive habitats, social scenarios provided by literature, theatre, movie, TV and music because they give us solutions to solve real social problems, poems with alexandrine lines because they signal an agile mind that can be useful for other more vital operations, or that is genetically correlated with other, heritable phenotypic traits (Thornhill 2003).

We further discussed that a reliable communication system is needed to maintain the usefulness of aesthetic valuations. The handicap principle is the most frequently cited mechanism to keep signals of quality honest. However, very often signals can be reinterpreted as cues or indices, which by essence cannot be cheated because they are physically linked with the advertised quality. Furthermore, for real signals previous interactions with the stimulus, either experienced by the beholder himself or by third parties, can be sufficient to avoid cheaters. Overall, the validity of the handicap principle remains to be supported empirically.

The handicap principle is nevertheless the only known mechanism controlling reliability that can explain evolution of extravagant ornaments such as the peacock tail. But as we will discuss in the next section, here again there is a more parsimonious explanation to evolution of such ornaments and of their associated preferences, provided that reliability is not assumed to be essential for communication systems.

### **X.3. Fisher's model of aesthetic preferences**

#### **X.3.1. Sexual selection without natural selection**

Sir Ronald Fisher was one of the greatest scientists of the twentieth century. In his history of mathematical statistics, Anders Hald called Fisher « a genius who almost single-handedly created the foundations for modern statistical science » (Hald 1998). His legacy deeply influenced various research areas such as agronomy, psychology, economics and evolutionary biology. In research on sexual selection, he is notably famous for the discovery of a particular mechanism explaining the co-evolution between sexual signals and the preference for these signals (Fisher 1915). Fisher observed that, once sexual signals and preferences have been paired, that is, once females start to prefer one particular trait in males, if the male trait and the corresponding female preference are both coded genetically then the corresponding genes will occur together in the chromosomes of offspring. At the population scale, the correlation between genetic variations for sexual signals and preferences will increase over generations.

Fisher thereby realised that traits and preferences would coevolve under the mere effect of their reciprocal action (Fisher 1915). Fisherian sexual selection is in marked contrast with the model of quality indicator, in which natural selection plays a preeminent role. Natural selection can be described as the sorting of individuals based on their match with their environment. For example, the ability of a male to resist parasites, to find preys or to escape predators, in sum, the ability to cope with its environment, signals the extent of direct and indirect benefits the male can provide to the female. In the model of quality indicator, sexual preferences are thus controlled by natural selection. In Fisher's model, sexual preferences are independent of natural selection.

Fisher's verbal assessment of signal-preference coevolution without natural selection had been covered with forgetfulness until Lande (1981) and Kirkpatrick (1982) formalised it mathematically in the eighties. These authors further documented the complexity and richness of the coevolutionary dynamics of signals and preferences. They showed that this dynamics depends on the relative strength of the genetic correlation between signals and preferences and the amount of genetic variations for those traits. Without entering into details, at the beginning of the coevolutionary process, the correlation is weak relative to the variation and both signals and preferences within a population converge to equilibrium. But as the correlation increases, the equilibrium becomes unstable and signals and preferences will coevolve away from it, in an arbitrary direction. This coevolution in an arbitrary direction is known as the "Fisherian runaway".

Like the quality indicator model, the Fisherian runaway can explain evolution of extravagant forms of signals and preferences that could reduce the survival of individuals. Proponents of the model of quality indicator view the peacock's tail as a handicap signalling masculine vigour. For those defending Fisher's model the peacock's tail epitomizes the outcome of a runaway process without natural selection. The model does *not* entail that natural selection is *not* influencing evolution of signals and preferences; it simply states that natural selection is not the mechanism fuelling extravagancy.

The strength of Fisher's model further lies in its ability to explain the tremendous diversity of sexual displays that occur in many species groups. Let's consider drakes. Drakes are highly colourful animals compared to female ducks, but even more stunningly they are very different from one species to another. The genus *Aix*, for example, includes two species, the Mandarin duck (*A. galericulata*) and the Wood duck (*A. sponsa*). In contrast to females, which are almost non-differentiable, males of these two species are very different, having in common only the fact to harbour multi-coloured patterns and modified feathers that have been selected for their beauty certainly more than for flight or thermoregulation. Natural selection can hardly explain such a diversification of signals. If the mechanisms producing pigments or shaping feathers were genetically linked to other vigour-related traits –a necessary condition for feather colours and shape to indicate quality– diversification of colours and shape would signify in-depth remodelling of the whole genetic make-up, which is unlikely to occur during the short evolutionary time that typically separates two sister-species.

Recently, it has been argued that Fisher's model is more than an alternative to the quality indicator model; it is the null model of evolution of sexual signals and preferences (Prum 2010). It is a null because it is the intersexual selection model that makes the minimum assumptions about evolutionary processes (Kirkpatrick and Ryan 1991). The quality indicator model is a complexification of this null model, which is not necessary to explain to most fundamental aspects of signal and preference coevolution (Prum 2010). As for any null model, if one cannot reject Fisher's model there is no good scientific reason to invoke alternative models.

### **X.3.2. Fisher's model and Darwinian aesthetics**

In 2003 a highly cited review article was published entitled "Darwinian aesthetics: sexual selection and the biology of beauty" (Grammer et al. 2003). By cataloguing supports to the preeminent role of health assessment in mate choice, the review actually



is a plea for the quality indicator model of aesthetics. The fact that this review was written by four leading evolutionary biologists illustrate how deeply rooted in the mind of evolutionists is the misinterpretation of Darwin's original view of sexual selection.

In his book on sexual selection, Darwin wrote he knew "of no fact in natural history more wonderful than that the female Argus pheasant should be able to appreciate the exquisite shading of the ball-and-socket ornaments and the elegant patterns on the wing-feather of the male" (Darwin 1871, p. 400). Darwin was more puzzled by the extreme refinements on feathers in this pheasant than by the length of its tail, which as in peacocks outrageously exceeds any functional requirement. Darwin hypothesized that these refinements are the evolutionary product of a selection for "agreeable partners" (Darwin 1871, p. 398) by females using their "taste for the beautiful" (Darwin 1871, p. 39,233). But Darwin was explicit that the "taste of the beautiful" serves no other functions than evaluating the intrinsic beauty of the partner: "The case of the male Argus Pheasant is eminently interesting, because it affords good evidence that the most refined beauty may serve as a sexual charm, and for no other purpose » (Darwin 1871, p. 516. By contrast, for Alfred Russell Wallace, a contemporary to Darwin who contributed to the birth of evolutionary biology, when sexual selection occurs « the only way in which we can account for the observed facts is by supposing that colour and ornament are strictly correlated with health, vigour, and general fitness to survive » (Wallace 1895). According to Helena Cronin, Darwin's view of mate choice as « a pure aesthetic experience, a selection and celebration of beauty for its own sake » (Cronin 1991) was one of the main points of disagreement between these two scientific eminences. She also highlighted that, although the scientific community has largely overlooked it, the model of quality indicator is entirely Wallacean, and anti-Darwinian.

Even though Darwin was the main discoverer of the process of natural selection, like Fisher he rejected its role of driver in evolution of sexual signals and preferences (Fisher 1915). According to Richard O. Prum, Fisher's model of coevolution between signals and preferences lays the groundwork for a genetic theory of true Darwinian aesthetics (Prum 2012). Interestingly, a recent model of quantitative genetics showed that the influence of the social environment on preferences (e.g., mate choice copying) could facilitate the initiation of the runaway process and increase the rate of trait elaboration (Bailey and Moore 2012). The importance of the social environment would be such that selection could occur in the absence of any genetic correlation between male signals and female preferences. This result broadens the scope of applications of the Fisher's model to many types of interactions between biological organisms. In the same vein, Prum suggested that Darwinian aesthetics could occur whenever a signal coevolves with its own evaluation independently of the effect of other evolutionary forces (Prum 2013). He argued that the coevolution of flower colours with pollinator preferences, of bird songs with female acoustic preferences, of artworks with the artistic sensibility of art dealers and museum visitors are all instances of aesthetic evolution. Similarly, for the neuroscientist Anjan Chatterjee art evolves autonomously (Chatterjee 2013). Art is varied and unpredictable when environmental pressures are relaxed. In oppressive regimes, or during periods of starvation, the diversification of art is constrained. For Chatterjee, if art were signalling something, this would be our freedom. This view of art evolution is entirely Fisherian.

To sum up, Fisher's model of coevolution between signals and preferences offers a parsimonious explanation to both evolution of extravagant ornaments and the diversity of signals and associated preferences. Fisher's model elaborates on original Darwin's

view of a sexual selection independent of natural selection. Fisherian signals do not indicate any quality of the emitter. Fisherian signals merely indicate that they exist and that a preference for these signals has coevolved with them. Consequently, Fisherian signals cannot be honest or unreliable, and thus no mechanism to maintain reliability is required in the evolutionary model of Fisherian aesthetics (Prum 2010, 2012).

Proponents of the Fisher's model of aesthetic evolution made a great step forward by recognizing that preferences are not all aesthetic. Signals coevolve with their own evaluations, but at the same time they can indicate a quality, which also influences their evolution (Prum 2010). Yet only the component of the preference that has evolved through a Fisherian mechanism would qualify as aesthetic.

In spite of its importance for sexual selection theory, I think that Fisher's model falls short in offering an encompassing explanation to evolution of aesthetics. As a coevolutionary model, it cannot account for the aesthetic experiences encountered with abiotic stimuli, such as beautiful landscapes. It may well be that the variety of aesthetic experiences springs from multiple and distinct evolutionary mechanisms. Or could it be otherwise? Maybe one can find an evolutionary model that can simultaneously encompass the universality and proteiform nature of aesthetic preferences and beautiful stimuli, the diversity of situations generating aesthetic experiences, and the distinction between preferences and aesthetic preferences. But first, let's have a look at what cognitive sciences have learned about aesthetics.

#### **X.4. Exploitative beauty**

##### **X.4.1. Universal beauty**

In order to support their claim that aesthetics could be investigated scientifically, all along the twentieth century empirical psychologists have looked for regularities in people's aesthetic responses to various kinds of stimuli. In a series of studies, Irvin Child and his colleagues presented people from different cultures (Americans, Central African, Japanese) with photos of various artworks (pictures of African masks and occidental sculptures, colour reproductions of abstract paintings; Child and Siroto 1965; Iwao et al. 1969). Importantly, Japanese and Central African people originated from remote places and were questioned to certify they had no knowledge of any sort on occidental art. Participants were asked to rank pictures according to the aesthetic value of artworks. Overall, these studies showed high correlations between rankings, in support to some universality in aesthetic preferences. Furthermore, they showed that the strength of correlations was increased when participants were art experts (art students for Americans, sculptors and other craftspeople for Africans and Japanese), thereby illustrating how familiarity with aesthetics promotes congruency rather than divergence in aesthetic preferences. It is likely that the shared component of aesthetic preferences is innate, grounded deeply within the biology of humans rather than being an acquired analogy. Many subsequent studies have concurred with this view that aesthetic preferences and beauty are, at least in part, universal and innate. We cited previously one study demonstrating that new-borns unanimously seem to prefer pretty-looking faces of all origins (Langlois et al. 1991). In the same vein, several studies have shown that infants from over the world share the same musical tastes, and that differences in adult's preferences are acquired culturally (Trehub 2000).

Empirical psychologists and visual scientists have conducted an impressive number of studies to identify which basic properties of stimuli, for example lines, colours, patterns, orientations and layouts, contribute to elicit a universally shared aesthetic response (for reviews, see for example Palmer et al. 2013). The first and foremost of such basic properties is symmetry. The link between symmetry and beauty can be traced back as far as Plato and Aristotle, but it is the mathematician George David Birkhoff who first formalized this link in its famous formulae  $M = O/C$ , where  $M$  is the aesthetic measure,  $O$  refers to order (mostly driven by symmetry for Birkhoff) and  $C$  to complexity. According to the formulae, for a given level of complexity the more symmetrical a stimulus, the higher the aesthetic measure is. Later, several psychological experiments confirmed the general importance of symmetry in aesthetic appreciation (Jacobsen and Hofel 2002; Palmer and Griscom 2013). People also tend to prefer shapes with curved contour more than similar shapes with sharp contours (Silvia and Barona 2009). For colours, vertical gradients with lighter and less saturated colours placed above darker and more saturated colours are rated more beautiful than the reversed gradients or than vertical patterns with randomly ordered colours (Valentine 1962). Higher-order spatial statistics of visual displays, which describes the general spatial organization of the display, also influence aesthetic preferences. In particular, scale-invariance usually increases the aesthetic appeal of visual displays (Redies et al. 2015). Scale-invariance means that similar patterns recur on finer and finer scales. By calculating Fourier spectral slopes on photos to estimate their scale-invariance, Christoph Redies and his colleagues found that artworks are more invariant than laboratory and household objects, parts of plants and scientific illustrations (Redies et al. 2007b). In accordance, faces represented in paintings and drawings from various cultures and periods typically are scale-invariant, while faces on ID-photos are not (Redies et al. 2007a). Regarding the representation of stimuli, people tend to prefer displays to the extent that they conform a categorical prototype (Rosch 1975). Preference for prototypes have been evidenced with all kinds of stimuli, ranging from simple abstract geometric forms (Winkielman et al. 2006) to surrealist paintings (Farkas 2002) and furniture (Whitfield and Slatter 1979).

It is noteworthy that, when investigated, these preferences that appear in humans independently of their culture have been found in other animals too. For beauty in general, Stefano Ghirlanda and his colleagues showed a shared preference for beautiful faces between chickens and humans (Ghirlanda et al. 2002). They trained chickens to peck at the picture of an average human face of one sex but not of that of the other sex. Then, they counted the number of pecks to images of new faces of both sexes. The authors found a very strong correlation between the number of pecks by chickens and rates of attractiveness for the corresponding faces obtained from university students. Regarding the characteristics of stimuli that are preferred, a number of studies have documented that, as in humans, symmetry increases the attraction of sexual partners (Swaddle and Cuthill 1994; Morris 1998), and that pollinating insects also prefer symmetric flowers (Møller and Sorci 1998; Rodríguez et al. 2004). But preference for symmetry also occurs for non-representational stimuli. In chickens, for example, naïve individuals (24-48 hours old) innately prefer asymmetric geometric forms, but a spontaneous preference for symmetric forms appears in normal rearing conditions within a few days (Clara et al. 2007). In another study, newly dark-hatched chicks consistently pecked more at round than at angular objects among 40 varied stimulus objects presented (Fantz 1957). Preference for prototypicality also is well documented in animals, notably by studies interested in the 'peak shift effect'. If a rat presented to a

square and to rectangle with a 4:3 aspect ratio is taught to be attracted to the rectangle, in testing trials it will respond even more strongly to a rectangle with a 3:2 ratio. This peak shift effect occurs because the rat learns to respond not to the rectangle itself but to rectangularity, that is, to what allows telling apart a rectangle and a square. The 3:2 is eventually preferred because it is more a prototype of rectangularity than a 4:3 rectangle is. Various examples of peak shift effects in animals have been reviewed by ten Cate and Rowe (2007).

Overall, the evidences presented hereinbefore unambiguously show that there exist preferences for particular characteristics of stimuli that are not specific to one domain<sup>4</sup>. Importantly, they also suggest that an aesthetic preference may not be a specific adaptation but it can be a by-product of adaptations in other domains. With the framework of the quality indicator model one would interpret preference for prototypical furniture as a by-product of adaptation to prefer feminine women and masculine men, and preference for round shapes as a by-product of preferences for round, energetic fruits, or round women breast, or any other good-quality round stimulus to which our ancestors have adapted. But from the quality indicator model these by-product preferences would not qualify aesthetical. Furthermore, this framework would not easily explain why aesthetical preferences are shared among species having very distinct reproduction systems or ecology such as among birds, primates and fishes. According to Darwin, the same stimuli “are often pleasing to widely different animals, owing to the similarity of their nervous systems” (Darwin 1872, p. 91). Darwin also thought that the diversity of aesthetic preferences could have a unique origin, a “fundamental cause in the constitution of the nervous system” (Darwin 1859, p. 255). In the next sections, I will present an evolutionary mechanism grounded in the neurobiology of organisms that can overarchingly explain both the universality and diversity of aesthetic preferences.

#### **X.4.2. The efficient processing theory of aesthetics**

One of the most important findings in psychology of aesthetics is that fluent processing of stimuli is hedonically marked and experienced as aesthetically pleasing (Reber et al. 2004). Besides, image statisticians and visual scientists have accumulated evidences that aesthetical visual stimuli such as artworks are coded more efficiently (i.e. both easily and precisely) than non-aesthetical ones (Redies 2008). Actually, the fluent processing theory and the efficient coding theory of aesthetics are two faces of the same coin: efficient coding is one neurobiological mechanism underlying the psychological phenomenon of fluent processing. In the following, I will use the expression Efficient Processing (EP) to designate both theories indistinctly. I will review a tiny fraction of the vast literature supporting the EP theory of aesthetics, starting with signal processing by low-level visual mechanisms and ending with cognitive mechanisms.

##### **X.4.2.1. Form processing**

Perception –the internal representation of the external world– primarily relies on sensory systems, which recode information contained in external physical stimuli into neuronal signals. The sensory systems of animals have adapted to process information efficiently, notably by removing the many redundancies that occur in natural stimuli

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<sup>4</sup> In cognitive sciences, a domain describes a category of problems that are repeatedly encountered throughout the life of an individual, e.g., finding mates, foraging, escaping predators.

(Barlow 1961; Simoncelli and Olshausen 2001). Colours, for example, are physically described by reflectance spectra, which indicate the proportion (relative to a white standard) of light reflected by the object surface at any wavelength. Within the range of visible light, reflectance spectra of natural surfaces are invariably characterised by a smooth shape indicating that spectral information at adjacent wavelengths is highly redundant (Cohen 1964). Theoretical models showed that the use of only three types of photoreceptors and the recombination of their outputs into two opponent channels, as they occur in humans, are optimal to efficiently encode spectral information (Buchsbaum and Gottschalk 1983). The sensitivity of retinal ganglion cells (the neurons that receive signals from photoreceptors) to light contrasts is another mechanism reducing redundancy, this time in the small (pixel) scale information of visual scenes (Barlow 2001). Indeed, it is more efficient to only encode the contour of a homogeneously coloured shape than to encode the very same information about the stimulus at every pixel within that shape. Further up in the visual system of primates, the retinal ganglion cells project to the Lateral Geniculate Nucleus (LGN), whose function is thought to reduce redundant information contained at a larger spatial scale, for example scale-invariance. Next, neurons from the LGN project in the brain to the primary visual cortex. Here, it was found that the neuronal network has adopted a sparse coding strategy: among the hundreds of thousands of neurons constituting this brain area, at any moment only a tiny fraction of them are simultaneously active (Olshausen and Field 2004).

These various adaptations to reduce or remove redundancies are not limited to the visual system of primates but also occur in other sensory systems, of nearly all organisms investigated so far, including invertebrates (e.g., Clemens et al. 2011; Zaslaver et al. 2015). In sum, visual scenes of natural environments, such as forested and grassy landscapes for primates, have large patches of homogeneous colours, are highly scale-invariant, have sparse distribution of light intensities throughout the scenes, and these characteristics have contributed to shape the visual system of humans and other animals (Simoncelli 2003; Field 1987).

A first series of evidence supporting the EP theory of aesthetics comes from studies conducted by two independent teams showing that artworks and natural visual scenes have similar statistical regularities (Graham and Redies 2010; Redies et al. 2007b; Graham and Field 2007). We cited previously that painted and drawn portraits are typically scale-invariant. More precisely, portraitists from all cultures represent faces with the degree of scale-invariance that is characteristic of natural scenes, which differs from the typical scale invariance of faces (Redies et al. 2007a). In general, artworks match more closely the level of scale-invariance of natural scenes than other man-made objects do (Redies et al. 2007b). Similarly, artists appear to approximate the sparse statistics of natural scenes (Graham and Field 2007; though in this case the luminance range of natural scenes had to be compressed to match that of art). Collectively, these results have been interpreted as evidence that stimuli mimicking the redundancies in visual representations of nature are more efficiently processed by the visual system, which increases their aesthetic appeal (Redies 2008; Graham and Redies 2010).

More direct evidence comes from psychological studies comparing aesthetic preference with ease of information processing. Symmetric and rounded shapes are spatially more autocorrelated than asymmetric and angular shapes, and as such they should be more efficiently processed by visual systems. This has been objectified in a study showing that people both responded quicker to symmetric and rounded shapes

and subjectively qualified them easier to process (Reber and Schwarz 2006). In another study, thousands of people from ten countries were administered a questionnaire on fine art preferences (Komar and Melamid, cited in Mather 2014, p. 128). The study confirmed that people over the world are highly consistent in terms of fine art preferences. Among other shared responses, people overwhelmingly agreed that art should be “relaxing to look at”.

#### **X.4.2.2. Content and context processing**

Besides redundancy reduction, another way visual systems have adapted to process information efficiently is by making expectations about the content of visual scenes, a phenomenon known as “predictive coding” (Rao and Ballard 1999). Predictive coding means that higher levels in the brain constantly send predictions about what to expect next in the flow of information processing. Predictions are compared with current input to establish prediction errors, which are sent back to higher levels that reevaluate their predictions, and so on. Predictive coding increases processing fluency by adapting low-level perception to the statistics of the perceived visual scene (e.g., top-down control of retinal receptive fields; Friston and Kiebel 2009).

In accordance with the EP model of aesthetics, psychological experiments revealed that the aesthetics of visual scenes with predictable content is valued positively. We already illustrated this with prototypes, which facilitate object categorisation. Furthermore, people prefer repeatedly presented stimuli to new stimuli they have never been exposed to before (Zajonc 1968). This co-called “mere exposure effect” is arguably the most studied phenomenon in empirical aesthetics, being supported by experiments with photographs, paintings, music, simple sounds, nonsense words or shapes (Bornstein 1989). The extent to which the layout of an object, beyond its mere identity, matches predictions also influences aesthetic preferences. For example, photographers know well that the vertical placement of an object should fit to its ecology for the whole scene to be aesthetically pleasing. Palmer and his colleagues (2012) demonstrated this by showing that people tend to prefer photos of flying eagles and of swimming sting rays where eagles and rays were placed at the top and at the bottom of images, respectively.

#### **X.4.2.3. Benefits and rewards of efficiently processed stimuli**

An important question for evolutionary aesthetics is *Why stimuli that are efficiently processed should be preferred?* It has been argued that such stimuli are selected because they are beneficial to the perceiver. Efficiently processed stimuli can provide the perceiver with direct benefits in at least three ways. First, EP enhances memory storing and retrieving. Both theoretical and empirical studies showed that sparse representations are more effective for storing patterns (Willshaw et al. 1969) and are advantageous for learning associations (Palm 2013). In the same vein, it was found that symmetrical patterns are remembered better than asymmetrical ones (Garner and Clement 1963). Second, EP increases speed of detection and recognition. High figure-ground contrasts, which have been shown to be aesthetically attractive in psychological experiments with humans, are also more efficiently coded than low figure-ground contrasts (Reber et al. 1998). In animals, there are numerous studies showing that conspicuous stimuli are advantageous to the perceiver (Renoult et al. 2016). For example, Spaethe et al. (2001) analysed the correlation between the colour contrast of

artificial flowers displayed on a green background and the time spent by bumblebees (*Bombus terrestris*) to visit three flowers of the same colour. The authors tested seven different colours and found that colour contrasts are linearly correlated with search time. Third, efficiently processed stimuli could save energy. Neural processing is extremely costly: in humans neural activity in the visual system alone accounts for 2.5 to 3.5 % of a resting body's overall energy requirements (Attwell and Laughlin 2001; Laughlin 2001). Simply opening the eyes onto an animated visual scene increases glucose consumption in the visual cortex by 50 % (Lennie 2003), which may explain why we expect to think more deeply when closing one's eyes. By minimizing the number of simultaneously active neurons, sparse coding allows metabolic savings (Olshausen and Field 2004). By shortcutting mid-level perceptual stages because lower level and higher levels are matching well, predictive coding is economical too (Friston and Kiebel 2009). Yet evidence that EP is metabolically beneficial is not evidence that efficiently processed stimuli allows significant energy savings. Indeed, whether or not energy savings have driven evolution of preference of efficient stimuli depends on how high is the differential cost between efficient and inefficient stimuli relative to the overall energy consumption of the aesthetic valuation. To my knowledge, such a differential cost remains to be evaluated.

Alternatively, efficiently processed stimuli may not provide the perceiver with direct benefits, but they could merely inform him that things and events are familiar and that interaction with the environment is going smoothly (Reber et al. 2004). As mentioned previously, EP is hedonically marked. This means that EP elicits a positive affective response; it is intrinsically pleasurable (Winkielman et al. 2003). In one study (Winkielman and Cacioppo 2001), participants were presented with pictures for which processing ease was manipulated by a subliminally presented contour prime that either matched or mismatched the target. Meanwhile, the affective response was monitored using facial electromyography. The authors found that easy-to-process pictures elicited higher activity over the region of *Zygomaticus major*, indicating positive affect. The hedonic marking of EP is consistent with the so-called affect-as-information theory (Clore et al. 2001; Schwarz 1990), where people unconsciously ask themselves "how do I feel about it" to decide whether processing should continue to complete recognition, scene evaluation and conscious decision making, whether a different perceptual strategy is required (for example attentional perception; Bradley 2009), or a motor response is urgently needed (for example escape; Ekman 1992). Pleasure is rewarding because it is triggered by a stimulus that is expected to be beneficial. As long as a stimulus is processed fluently, our brain is rewarded with pleasure, which drives us to behave positively with that stimulus.

Eventually, processing efficiency both directly benefits the perceiver and informs him about the potential benefits of the stimulus. Importantly, the pleasure generated by efficient processing is in itself rewarding. Thus formulated, the EP model of aesthetics does not seem to differ markedly from the quality-indicator model of aesthetics. There is one fundamental point, however, that puts apart these two models: while in the former the adaptation is the specific preference, in the later the adaptation is the general processing strategy. Because of that difference, EP stimuli can undergo a completely different evolutionary dynamics compared to quality-indicator stimuli.

### X.4.3. The exploitation of efficient processing

In sexual selection theory, besides the models of quality indicator and of Fisherian runaway, there is a third model of preference and signal evolution that has gained popularity over the last two decades: the exploitation of sensory biases (Ryan et al. 1990; Ryan and Rand 1993; Endler and Basolo 1998). The model assumes that adaptations of sensory systems to various tasks, such foraging, escaping predators or finding mates, generate preference biases, and that sexual signals exploit these biases to increase the attractiveness of the signaller. Generally, low-level mechanisms of sensory systems are tuned to the dominant physico-chemical characteristics of that environment. In aquatic habitats, for example, lighting is highly variable, depending on water depth and bank vegetation. Different studies on fishes independently reported an adaptive tuning of photoreceptor sensitivities to the specific lighting environment of the studied species (e.g., Cummings and Partridge 2001; Bowmaker et al. 1994; Carleton 2009). Sexual signals can then adapt to the specific photoreceptor sensitivities to increase conspicuousness or distinctiveness (e.g., Cummings 2007). Some preference biases can originate from higher-level perceptual mechanisms than those of the sensory systems. Males in several species of Goodeinae fishes, for example, display a terminal yellow band on their tail, which attracts females by mimicking a worm on which these fishes feed (Garcia and Ramirez 2005). Here, the exploitation of a preferential bias requires at least configural perception for the female's brain to identify a worm, and possibly cognitive recognition. In order to account for preference-biases originating from high-level perceptual mechanisms, several authors have renamed the expression "sensory bias" as "perceptual bias" (Ryan and Cummings 2013; Schaefer and Ruxton 2009).

The exploitation of EP model of aesthetic evolution proposes that aesthetic stimuli exploit receiver's innate attraction driven by EP. Painted portraits that are aesthetically valued owing to their spatial statistics mimicking those of natural scenes are like tail yellow bands exploiting female's attraction to yellow worms in Goodeinae fishes. Crucially, the exploitation of EP simultaneously fits to models of sensory, perceptual and cognitive bias<sup>5</sup> since EP influences any stage in information processing, from perception to cognition. Because of this, EP-driven preferences can be highly diversified. The exploitation of EP model thus predicts a very dynamic "landscape" of aesthetic preferences, which is likely to vary among species, populations, individuals and also with time for a given individual. In return, such a dynamic landscape would promote diversification of signals (Arnold et al. 2001). In addition, the model predict a rugged landscape of aesthetical preferences: by combining different aspects of form, patterning, colouration, layout, symbolic meaning and contextual presentation, there are multiple ways a signal can be efficiently processed, and thus multiple opportunities to bypass any ecological, phylogenetic or physiological constraint to signal diversification. This is noteworthy because a recurring criticism to the model of sensory bias refers to its inability to explain the diversity of sexual signals. Richard O. Prum wrote "sensory bias seems to me unlikely to explain the bulk of secondary sexual trait and preference radiation in groups of closely related species" (Prum 2012). While this is likely correct for most sensory biases, the exploitation of EP model predicts the exact opposite

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<sup>5</sup> In Ryan and Cummings (2013), perception encompasses cognitive mechanisms. I added the expression « cognitive bias » to follow the distinction between perception and cognition I made throughout the review, in accordance with the dominant view in empirical aesthetics.



pattern: an extreme diversification of both signals and preferences.

By essence, the exploitation of EP cannot be co-evolutionary. However, according to the EP theory of aesthetics, the positive aesthetic value of a stimulus can sprout from the co-evolution between this stimulus and its associated preference. Let's consider a stimulus that coevolves with its preference following quality-indicator and Fisherian mechanisms. From a brain perceptive, this stimulus would trigger pleasure, which would activate desire, which may eventually drive the perceiver to interact with the stimulus. According to the exploitation of EP model, this pleasure and the associated preference initially have no aesthetic value. But the coevolutionary loop allows perception and cognition to adapt to efficiently process the stimulus. Because it is hedonically marked, EP would then add pleasure to pleasure, thereby reinforcing preference for the stimulus. Here, the added pleasure is aesthetical. But it is only if the stimulus further mimics the form, colour, pattern or any other characteristic of other important stimuli that have also shaped perception and cognition, that the stimulus will be exploitative and would become beautiful. The EP theory of aesthetics thus identifies the aesthetic preference as one component of the overall preference for a stimulus. The evolutionary model of exploitation of EP interacts with other models of stimulus evolution to increase further the relative contribution of aesthetics in preference.

The exploitation of EP extends previous suggestions that aesthetic preference is a by-product of evolution and development of sensory systems. Modelling the evolution of artificial neuronal networks, Arak and Enquist (1993) showed that preference for exaggerated stimuli could emerge from the mere adaptation of sensory systems to recognize signals, and the authors already qualified such by-product preference as aesthetical. In chickens, it was found that preference for symmetry arises early during development as a by-product of the improvement of pecking sensorimotor skills that occurs during active food manipulation (Clara et al. 2007). This result confirms predictions from another theoretical work by Enquist and Arak (1994) showing that symmetry preferences is a by-product of the need to recognize objects irrespective of their position and orientation in the visual field. The EP theory of aesthetics offers a functional explanation to these results and recasts them into a more general paradigm that also accounts for other universal and domain-independent preferences.

The model of exploitation of EP proposes a dynamic of aesthetic evolution that can uniquely explain most if not all of the often-observed correlations between exploitative stimuli and quality. It is usually assumed that preference biases pre-date preference for quality indicators (Kokko et al. 2003). In the case of the Goodeinae fishes, for example, the appearance of feeding responsiveness during evolution likely predated that of sexual responsiveness (Garcia and Ramirez 2005). Yet the observation that feeding responsiveness decreases in species with more elaborated yellow band tails suggests that the originally exploitative band tails subsequently evolved into honest signals (Garcia and Ramirez 2005). Such a transition between models is nevertheless permitted only if mechanisms underlying exploitative stimuli are functionally linked with mechanisms determining quality (e.g., an increase in saturation of the yellow band simultaneously increases resemblance with worms and indicates ability of males to find food-derived yellow carotenoids in their environment). Unfortunately, such functional links are often speculative and sometimes physiologically unsupported. By contrast, the exploitation of EP model does not require any functional link to explain correlations between stimuli and quality. In red-legged partridge (*Alectoris rufa*), for example, a higher fractal dimension of bib predicted better body condition and immune responsiveness (Pérez-Rodríguez et al. 2013). This result is puzzling if one thinks fractal

dimension as an indicator of quality because there is no obvious functional link between the studied qualities and the mechanism regulating the spatial structuring of melanin deposition in feathers. However, it is easily explained by EP exploitation: high bib fractality would have evolved secondarily to increase female preference by exploiting the hedonic marking of fractal patterns, which is a by-product of the general adaptation of bird visual system to the spatial statistics of natural environments.

#### **X.4.4. Pleasure, desire and disinterestedness**

The EP theory of aesthetics and the evolutionary model of EP exploitation echo a prominent concept in philosophy of aesthetics: disinterestedness. Although it can be tracked down to the writings of many philosophers including Schopenhauer (“pure, will-less contemplation”), Croce or Bergson, the concept of disinterestedness culminated in Kant’s aesthetics (Kant 1790/1987) to a point that the experience of feeling a pleasure free from any utilitarian strings usually refers to “Kantian” aesthetics. For those philosophers, then, aesthetics is linked to pleasure and not to any form of desire. It is an entirely hedonic experience. In colloquial parlance, the aesthetic experience could be described as “liking without wanting” (Chatterjee 2003).

The disinterestedness of aesthetics has been germane to many works and theories in experimental aesthetics (e.g., Palmer et al. 2013). In turn, the neurosciences gave scientific credit to the philosophical concept by revealing distinct neurophysiological bases to pleasure and to desire (Berridge et al. 2009). In mammals, pleasure engages an ensemble of brain regions collectively labelled the limbic system. Crucially, the neural circuitry of pleasure is the same for the different stimuli and sensory modalities: the view of good food, the taste of a thirst-quenching drink, the listening of a charming voice, or any other advertisement of potential benefits are all regulated by the same opioid and cannabinoid neurotransmitters in the limbic system (Chatterjee 2013). The limbic system is also the place that gives birth to desire. However, desire is mediated by a different chemistry: the dopamine system. Usually, pleasure motivates us to act through the effect of desire. Both affects are tightly linked and are thus shaped conjointly through evolution and development (Chatterjee 2013). Yet because they are regulated by different neurochemical mechanisms, in some cases they may activate disjointedly. Dopamine-activating drugs, like amphetamine, for example, amplify desire but not liking. In extreme cases, the disjunction may lead to addiction (Robinson and Berridge 2008). According to Chatterjee, amplification of pleasure without desire, that is, brain flooding with opioids and cannabinoids but not with dopamine is the neurophysiological mechanism underlying a true, disinterested aesthetic experience (Chatterjee 2013). It is thus a quest for pure pleasure that drives people to art exhibitions, motivates us singing alone in the shower, makes us doodling friezes on the corner of a sheet during boring meetings.

It is noteworthy that Darwin had already envisioned this link between pleasure and beauty: “... the sense of beauty in its simplest form - that is, the reception of a peculiar kind of pleasure from certain colours, forms [...]” (Darwin 1859; p. 255). As emphasized by Michel Kreutzer, “taste” in the expression “taste for the beautiful”, which is repeatedly used by Darwin to characterise the main motivation in mate choice, was referring back to a eighteenth century concept of beauty linked to immediacy and disinterestedness (Kreutzer and Aebischer 2015). Darwin’s view of mate choice as a selection for beauty for the sake of pleasure in beauty was thus fully consistent with a modern mechanistic definition of aesthetics.

Crucially, the evidences supporting the core role of pleasure and the lack of utilitarian goal in human aesthetics have been recently found in animal brains too. Firstly, researches on the neurobiology of aesthetics are not restricted to humans: pioneering studies on the dissociation between pleasure and desire, for example, were conducted on rats (Berridge et al. 2009). Secondly, the underlying limbic neural mechanisms for generating affective reactions are similar in the brains of most mammals (Berridge and Kringelbach 2008), and the general architecture of the limbic system is relatively conserved among tetrapod, at least (Bruce and Neary 1995). The biological grounds to aesthetics described previously are thus likely common to mammals, birds, reptiles and amphibians. Last, a recent study with fruit flies *Drosophila melanogaster* showed that, in these organisms too, liking and wanting can be uncoupled and are controlled by different neural circuitries (Lin et al. 2014). From a biological perspective, there is therefore no good reason to expect the aesthetic experience to be unique to humans.

Efficient processing is only one of the many mechanisms in which liking can occur without wanting. Rolf Reber emphasized that, “although the fluency theory covers some interesting phenomena, it does not cover all kind of aesthetic experience” (Reber 2012). For example, solving conceptually challenging tasks, like understanding how a porcelain urinal (*Fountain*, Duchamp, 1917) has become one of the most important pieces in 20th-century art, can also generate pleasure in the form of aesthetic experience (Redies 2015). Aesthetic experience also accompanies solving of processing tasks early in the visual system, for example when the shape of an object in a noisy image suddenly appears (Topolinski et al. 2015). These two types of aesthetic experiences are not entirely explained by efficient processing: although pleasure is triggered precisely when information processing becomes fluent, here the ambiguous, challenging nature of the stimulus is also determining. I suggest that the exploitation of EP is one particular case of a more general mechanism of aesthetic evolution through exploitation of pleasure mediated by the dynamics of information processing. Nevertheless, because EP can be modelled or approximated (see paragraphs on image statistics) for a diversity of stimuli and animal species, in my eyes the exploitation of EP offers a highly promising and workable model for evolutionary aesthetics.

## **X.5. Conclusions**

Few topics can take pride in transcending the traditional frontiers between disciplines from the humanities and the sciences as much as aesthetics. It is only recently, however, that cognitive sciences have realised how much they could gain in recognizing two millennia of thoughts about aesthetics in philosophy and the arts (Shimamura and Palmer 2012). Now that evolutionary biology is getting involved in the topic too, it is vital that the discipline builds on existing knowledge, both for its credibility and for the quality of its contribution.

In an attempt to broadly define the contours of aesthetics I first listed some necessary (but not sufficient) criteria that could characterize this concept: (1) the aesthetic experience is ubiquitous: it can be caused by a variety of stimuli, both biotic and abiotic, from different domains; (2) beautiful stimuli in a given domain are highly diversified; (3) they are also often extravagant; (4) yet it seems that individuals within

and even across species share a common taste for the beautiful. I then reviewed three main models of aesthetic evolution, discussing how they could address these criteria. The most widely cited model of quality indicators could easily explain the ubiquity and the shared component of aesthetic experiences, as well as the extravagancy of some beautiful stimuli. However, it hardly explains the huge diversity of beautiful stimuli within a domain. Fisher's coevolutionary model of aesthetics can account for both the diversity and the excessive elaboration of beautiful stimuli. However, it is difficult to understand how this model alone could maintain shared aesthetic preferences. Moreover, Fisher's model being exclusively coevolutionary, it does not explain temporal changes in abiotic beautiful stimuli.

The third model I reviewed assumes that aesthetics is a by-product of adaptations to process and to be attracted by certain stimuli in the brain of the perceiver. Throughout their evolution, the perception and cognition of animals have evolved to efficiently process and to find beneficial stimuli pleasurable. Efficient processing and the associated pleasure are adaptations determining attraction or preference (in choice situation) that could evolve following quality indicator or Fisherian models. But being attracted by or preferring a stimulus does not signify we find this stimulus beautiful. Beauty arises if the stimulus exploits efficient processing and pleasure, if it taps into these adaptations to amplify their effect. The exploitative phenomenon occurs when stimuli have formal and contextual presentation and meaning that can simultaneously activate several of such adaptations. This model of exploitation of efficient processing, and more generally of processing-driven pleasure, can successfully explain the ubiquity and universality of aesthetic experiences, and the diversity and extravagancy of beautiful stimuli.

In evolutionary biology, aesthetics has been traditionally defined *a posteriori* from the putative mechanisms of its evolution. I fully acknowledge that definitions should emerge from results rather than merely stick to postulates. But it is an epistemological fallacy to try to understand the evolution of something that has been defined as the result of its evolution. It is like trying to understand how the wings of birds have evolved while defining wings as adaptations to flight. Surely this approach would strongly narrow the spectrum of possible mechanisms influencing wing evolution. Arguably a better approach would define wing from scientific results on empirical, proximate mechanisms making a avian wing what it is, for example its lift and the presence of feathers. Listing necessary but not sufficient criteria as I did in the introduction crudely followed this empiric approach to definition. And as we could see, it already permitted to highlight some limitations of major models of aesthetic evolution. The exploitation of EP model not only fits to the listed criteria; it is also soundly grounded into a bulk of empirical works on aesthetics. The model naturally emerged from results showing that beautiful stimuli are processed efficiently (the EP theory of aesthetics) and activate the pleasure circuitry independently of the desire circuitry. When applied to sexual selection, the exploitation of EP also recognizes that aesthetic preference is different from (and nested within) sexual preference. This difference is critical to understand evolution of aesthetics and its role in evolution of communication, but unfortunately it could not but be ignored by presupposedly defining aesthetics as an adaptation. Last, the EP exploitation model of aesthetic evolution has no ambition of durability. Empirical aesthetics has become a very active field of research, and it will be a necessity for evolutionary biologists to adapt and refine models of aesthetic evolution as knowledge in this field progresses.

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