An Introduction on Formal and Computational Models in Popular Music Analysis and Generation

Moreno Andreatta and Gilles Baroin

Abstract This article provides a first introduction to some formal and computational models applied in the analysis and generation of popular music (including rock, jazz, and *chanson*). It summarizes the main philosophy underlying the project entitled "Modèles formels *dans* et *pour* la musique pop, le jazz et la chanson", which constitutes one of the research axes of the GDR ESARS (Esthétique, Art & Science). Initially conceived as an extension of the MISA project carried on by the Music Representation Team at IRCAM, this research axis aims at bringing together researchers from different horizons, from the traditional MIR community of Music Information Retrieval to the most sophisticated approaches in mathematical music theory and computational musicology. It also includes an epistemological and critical evaluation of the relations between music and mathematics, together with some programmatic reflections on the possible cognitive and perceptual implications of this research.

Introduction

There is an increasing interest within the computational musicological community for formal and computational models applied not only in the analysis but also in the generation of popular music. With this label, one generally includes repertoires—such as rock, jazz, and *chanson*—which are not considered as belonging to the art or contemporary music.[1] The common point among all formal and computational methods

---

[1] This paper summarizes some aspects of this project that have been described in details in Andreatta (2014a). For a pedagogical and large-public introduction to mathematical models in popular music, also see Andreatta (2014b). A more technical presentation of the main concepts described in this paper and addressed to the community of researchers working on computational musicology is given in Bigo and Andreatta (2015).

M. Andreatta (✉)
IRCAM/CNRS/UPMC & IRMA/GREAM/Université de Strasbourg, Strasbourg, France
e-mail: moreno.andreatta@ircam.fr

G. Baroin
ENAC & LLA Creatis/CNRS, Univ de Toulouse, Toulouse, France
e-mail: gilles@baroin.org

Z. Kapoula and M. Vernet (eds.), *Aesthetics and Neuroscience*,
DOI 10.1007/978-3-319-46233-2_16

described in this article relies on the relevance of the interplay between geometric and algebraic approaches in music theory, analysis and composition.[2] This postulate applies equally well to contemporary art music and popular music repertoires, which opens interesting questions about the possible articulations between these two study domains.[3] Moreover, the tools described in this paper also apply to the field of folk or traditional music, which is—according to a programmatic article by Philip Tagg on theoretical, methodological and practical aspects of popular music studies (Tagg 1982)—one of the three possible kinds of music (together with classical or art music and popular music).[4] This is possible thanks to the flexible nature of geometric representations, which enable to grasp equally well the logic behind the songs and "chansons", from The Beatles to Paolo Conte, as well as the harmonic construction of rock/pop pieces (from Frank Zappa's to the songs by Depeche Mode).[5] After briefly describing some theoretical aspects underlying the geometric representations used in the field of computational (popular) music analysis, we will show some new visualisations of musical structures and processes

---

[2] According to the Field-medallist Alain Connes, "concerning music, it takes place in time, like algebra. In mathematics, there is this fundamental duality between, on the one hand, geometry—which corresponds to the visual arts, an immediate intuition—and on the other hand algebra. This is not visual, it has a temporality. This fits in time, it is a computation, something that is very close to the language, and which has its diabolical precision. […] And one only perceives the development of algebra through music" (Connes 2004). This duality constitutes a major common point between music and mathematics, allowing proposing a common basis for the creative processes in both fields of music and mathematics, as suggested by Alain Connes in his dialogue with Pierre Boulez on creativity in mathematics and music (Boulez and Connes 2011). See Andreatta (2010) for a detailed description of the "mathemusical" research that has been carried on in the last ten years within the MISA project (*Modélisation Informatique des Structures Algébriques en musique*), with a special emphasis on the interplay between algebra and geometry. See Andreatta et al. (2013) for a description of a category-oriented framework for describing the creative process in music and mathematics.

[3] This question has been explicitly addressed in the conference "Musique savante/musiques actuelles: articulations" (Contemporary art music/popular music: articulations), hosted by IRCAM and organised under the auspices of the French Society of Music Analysis, in collaboration and with the financial support of the IReMus (Institute of Research in Musicology, UMR 8223, Paris-Sorbonne) and the BPI of the Centre Georges Pompidou and with the participation of the French component of IASPM (International Association for the Study of Popular Music). The Proceedings are forthcoming in a special issue of the multimedia online journal *Musimédiane* (Andreatta 2016). For a first attempt at analysing the necessity of substituting this typology with a finer taxonomy based on computational models focusing on musical objects and making use of different theoretical approaches in order to carry on computer-aided music analysis, see Bergomi et al. (2015).

[4] This typology constitutes what Tagg calls an *axiomatic triangle* of musical genres, each of which being characterized by criteria such as the usual or unusual mass distribution, the existence of a circle of professionals or a circle of amateurs who produces and transmits it, the principle modality of storage and distribution (ranging from oral transmission, in the case of folk music, to the recorded sound, in the case of popular music), the anonymous versus authorial character of the underlying compositional process, and so on.

[5] For a recent analytical application of the formal tools discussed in this paper from the perspective of a geometric-based automatic classification, see Bergomi et al. (2015).

making use of a recent model providing some additional tonal information with respect to the traditional *Tonnetz* representation.[6]

Geometric Representations of Musical Structures and Processes

Although sometimes very far from a stylistic point of view, there are pieces belonging to the rock, pop and "chansons" repertoire which somehow share the same "musical logics" concerning the harmonic organization. More precisely, if one restricts the analysis to consonant chords (major and minor), it is possible to find interesting common points between stylistically-different pieces in the way in which the chord progressions are constructed. In order to make these similarities evident, the (computational) music analyst can use several geometric representations of harmonic spaces, including the circular representation, the different types of *Tonnetze*, the orbifolds, the spiral array and many others.[7]

In this paper we will focus on the *Tonnetz*, a geometric representation of the pitch space originally proposed by Euler (1774) in the second half of the XVIII^{e} century as an alternative to the well-established circular representation previously introduced by Marin Mersenne in his *Harmonie universelle* (Mersenne 1636).[8]

The *Tonnetz* is a symbolic organization of pitches in the Euclidean space defined by infinite axes associated with particular musical intervals. Although these graph-theoretical representations have been rediscovered later by music theorists, musicologists, and composers (including Arthur von Oettingen, Hugo Riemann and Henri Pousseur), the interest of the computational musicology community for this type of structure is very recent. The model is currently used to represent chord

---

[6] Two main models, the "Polarized Tonnetz" and the "Spinnen Tonnetz", originally conceived by Hugo Seress and Gilles Baroin, represent a very interesting way of integrating some tonality-based constructions within transformational music analysis. For a critical presentation of these two models and their comparison with other tools belonging to the transformational musical analysis tradition, see Seress and Baroin (2016).

[7] See Bigo (2013) and Bigo and Andreatta (2015) for a historical description of the main geometric representations in computational music analysis. Algebraic topology has provided a very elegant theoretical framework for describing all these representations, as shown by Bergomi (2015) in his recent doctoral thesis.

[8] The reader interested to learn more about the three main contributions of Leonhard Euler (as a mathematician, physicist and music theorist) can refer to Hascher and Papadopoulos (2015).

progressions within the so-called neo-Riemannian transformational approach,[9] whose application includes post-romantic tonal music (Cohn 2012) but also rock, jazz and pop music repertoires (Capuzzo 2004; Hascher 2007; Briginshaw 2012; Bigo and Andreatta 2015). From a generative perspective, this model has also been used in contemporary music (for example by the French composer Jean-Marc Chouvel), as well as in popular music contexts, leading to a geometrically constrained-based series of Hamiltonian Songs (Andreatta 2014b; Bigo and Andreatta 2014).[10]

Mathematically-speaking, the circular representation and the *Tonnetz* are equivalent ways of formalizing in an algebraic way the structural properties of the equal-tempered system (i.e. the division of the octave into twelve equal intervals, as in the piano). The main computational property is the possibility of generating the system by using combinations of major third (i.e. four semitones) and minor third (i.e. three semitones) intervals, as depicted in Fig. 1.

As the previous figure suggests, we are interested in the computational aspects of the geometric representations, and in particular in the fact that they can be implemented in programming languages for computer-aided music analysis and composition. For example, to compute the compactness of harmonic trajectories in different automatic-generated *Tonnetze*, the computational musicologist has a new geometric way of handling the problem of style classification, which is one of the most interesting research areas in Music Information Retrieval. We will not enter here into this aspect of our research, which has been largely addressed in several recent contributions (Bigo et al. 2013; Bigo and Andreatta 2015; Bergomi 2015; Bergomi et al. 2015), but we will focus on visualisation techniques as applied, in particular, to popular music repertoires. Figure 2 shows the *Tonnetz* as generated by three musical operators (P, R and L), corresponding to the three possible ways of transforming a major chord into the corresponding minor chord having two notes in common with the initial chord. These operators are respectively called the “parallel” (indicated by P and transforming, for example, the C major chord into the C minor chord, and vice versa), the “relative” (indicated by R and transforming, for

---

[9] Neo-Riemannian music analysis is a formal methodology developed after the writings by the German music theorist Hugo Riemann (1849–1919). Following David Lewin’s transformational turn in music theory and analysis (Lewin 1987/2007; 1993/2007), which integrates neo-Riemannian techniques within a much more general approach, one may speak about neo-Riemannian transformational music analysis as a structural methodology combining the two independent approaches. See Gollin and Rehding (2014) for a comprehensive textbook on Neo-Riemannian analysis.

[10] Hamiltonian Songs are so-called after the Irish physicist, astronomer, and mathematician Sir William Rowan Hamilton (1805–1865). In graph theory, a Hamiltonian cycle is a path passing through all possible nodes of a graph and ending precisely where it started. It is well known that there are exactly 124 Hamiltonian cycles in the *Tonnetz* (Albini and Antonini 2009) which can be classified by using their inner symmetries (i.e. the possibility of decomposing a given cycle into sub-sequences that repeat identically in order to generate the entire cycle). The complete list of Hamiltonian cycles with some examples of Hamiltonian Songs is available at: http://repmus.ircam.fr/moreno/music.

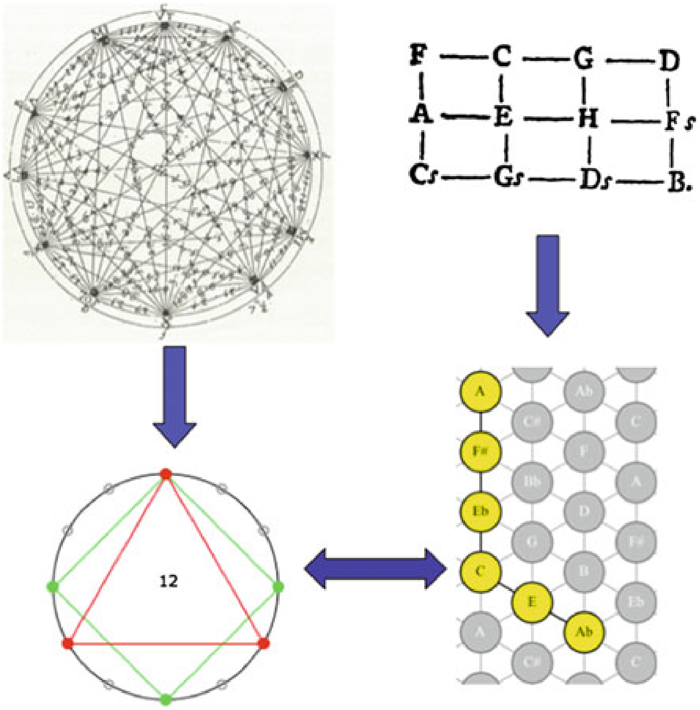


Fig. 1 Two mathematically equivalent representations of the family of pitch-classes within the equal-tempered system: the circular representation, whose origin goes back to Mersenne (*on the left*) and the "Speculum Musicum" by Euler, which is the ancestor of the *Tonnetz* (*on the right*). The circular representations and the *Tonnetz* are obtained respectively by using the OpenMusic visual programming language (see Agon 2004) and the *Hexachord* software (see Bigo 2013)

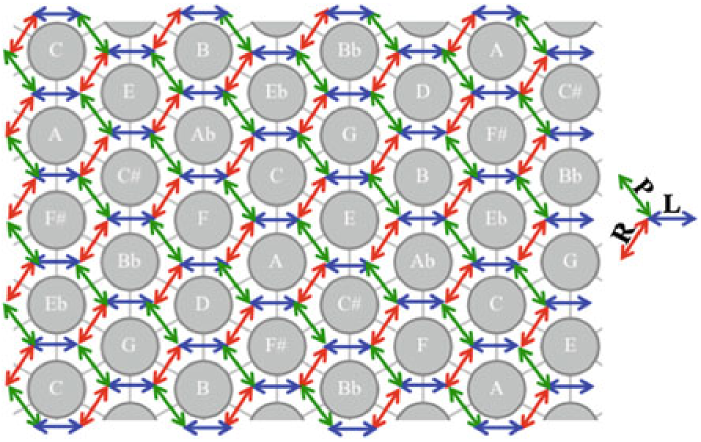


Fig. 2 The *Tonnetz* as a hexagonal tiling of the plane where each major (respectively minor) chord is transformed into three minor (respectively major) chords via the three P, R L operators preserving two of the three notes of the initial chord

example, the C major chord into the A minor chord, and vice versa) and the "leading-tone" (indicated by L and transforming, for example, a C major chord into a E minor chord, and vice versa).

Circular Representations and Tonnetze for Popular Music

In order to show how the circular representation and the *Tonnetz* constitute two complementary approaches in the analysis of harmonic progressions, let us stress a little bit more the relevance of the notion of symmetry in music. An interesting starting point is provided by two stylistically different pieces having the same

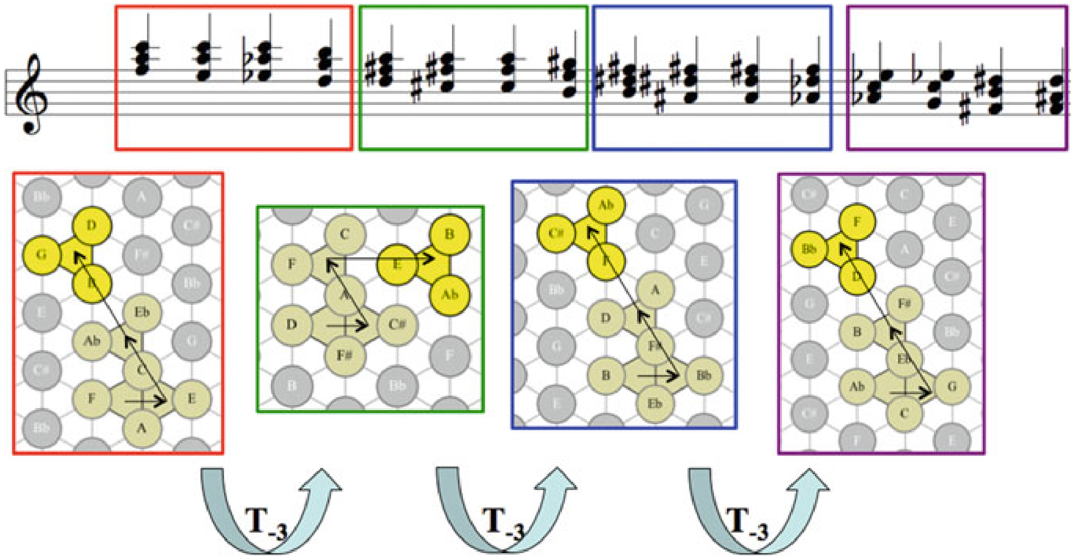


Fig. 3 Harmonic progression in Zappa's piece *Easy Meat*, seen as a series of transpositions (of a minor descending third T_{-3}) of a same cell (the first one, in *red*). The four cells generate therefore the same trajectory in the *Tonnetz* (where apparently different shapes correspond in fact to the same trajectory because of the toroidal structure of the *Tonnetz*) (color figure online)

"spatial" logics with respect to the harmonic organisation: *Easy Meat* by Frank Zappa and *Madeleine* by Paolo Conte.

Let start with Zappa's piece *Easy Meat* and one of the most recurrent harmonic progression in the piece.[11] This progression, shown in Fig. 3, contains sixteen chords and can be decomposed as a repetition (via the transposition operation) of a given cell of four chords. Each cell contains the same series of neo-Riemannian operators, as Fig. 4 shows.

The figure shows the progression represented in an unfolding *Tonnetz* representation conceived by Gilles Baroin, corresponding to the two-dimensional projection of his *Hypersphere of Chords* (Baroin 2011). In this case the trajectory of a cell is rigorously translated in space, metaphorically providing a kind of composer's "signature" for the piece.

It is interesting to compare this type of chord progression with a different harmonic progression used by the Italian "chansonnier" Paolo Conte in his piece entitled *Madeleine*. In this song, the harmonic progression of the verse, repeated several times all along the piece, is also constructed in a similar way. There are four blocks, the first three of which are obtained by transposing an initial cell by an ascending third. They therefore correspond to a same trajectory in the *Tonnetz*, whereas the symmetry breaking due to the fourth block, structurally different from the three previous ones, enables the chord progression to come back to the initial chord. This progression is given in Fig. 5.

---

[11] The interest of using Neo-Riemannian techniques to analyse this passage has been originally pointed out by Capuzzo (2004).

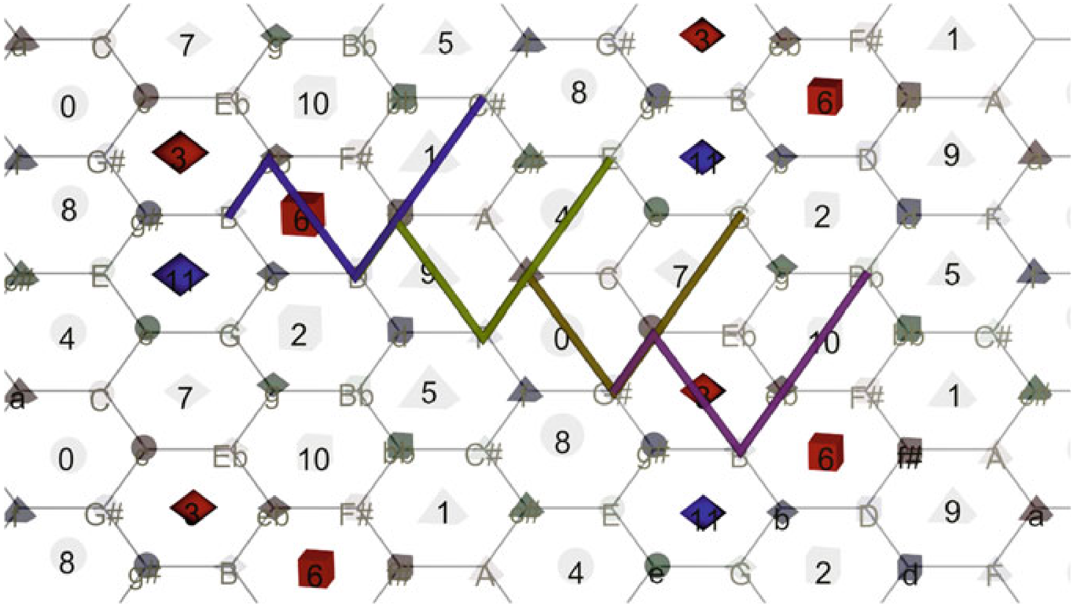


Fig. 4 Zappa's "signature" for the piece *Easy Meat*, represented in Gilles Baroin's visualisation of the *Tonnetz*

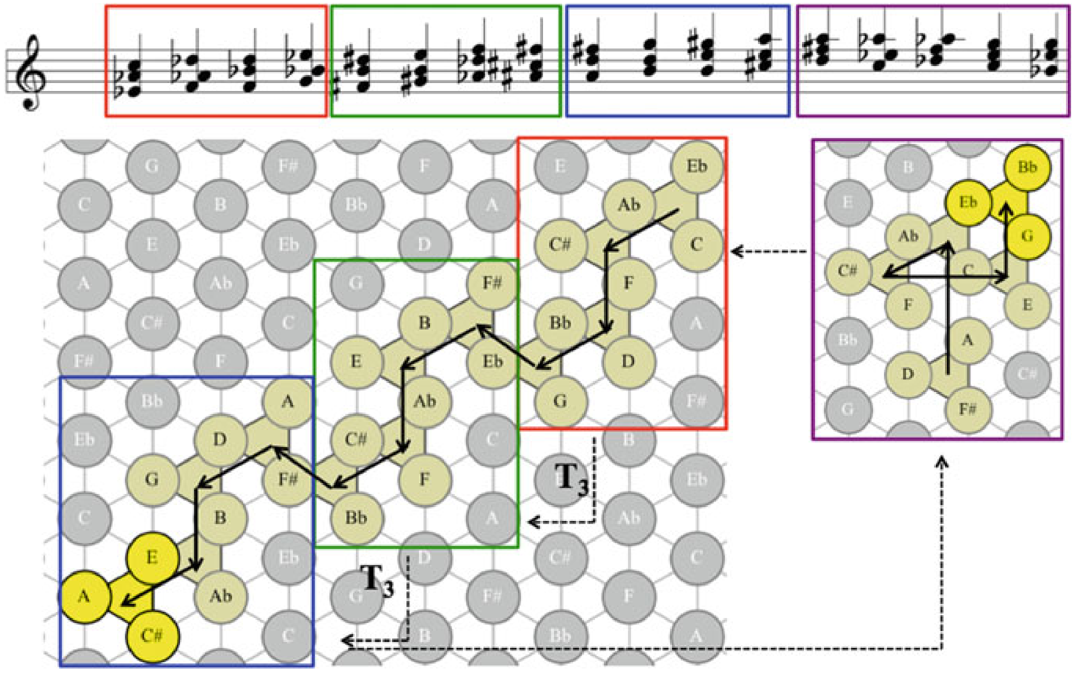


Fig. 5 Harmonic progression used by Paolo Conte in his song *Madeleine* represented as a series of spatial translations of an initial cell containing four chords. The fourth cell, containing five chords, functions as a new trajectory "forcing" the progression to come back to the initial tonality

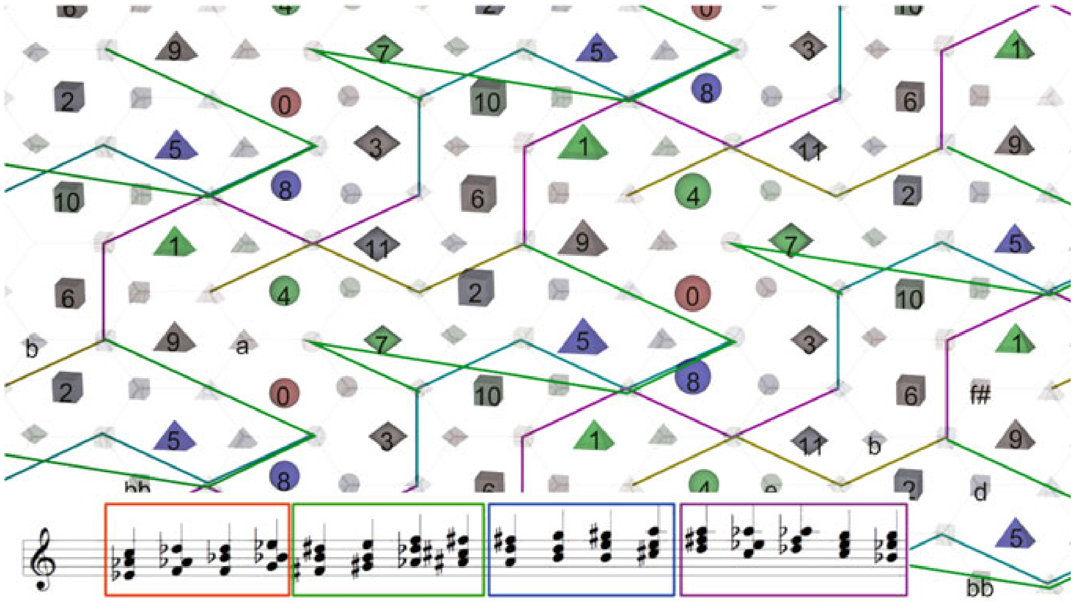


Fig. 6 The “almost perfect” covering of the harmonic chromatic space by major chords and their transpositions in Paolo Conte’s *Madeleine*

Despite this superficial analogy between the two pieces, the compositional process in *Madeleine* has a remarkable property which makes the chord progression “qualitatively” very different from that used by Zappa. In fact, up to a single chord, which is missing, it constitutes a *covering* of the chromatic space by major chords and their transpositions. This covering property is much more evident in the following *Tonnetz* representation provided by Gilles Baroin (Fig. 6).

In other words, the harmonic progression of the piece corresponds to a trajectory which passes through (almost) all twelve major chords (with repetitions). This property admits a natural mathematical generalization by considering the traditional *Tonnetz* as a graph whose vertices consist of all major and minor chords and by studying trajectories passing only once through all major and minor chords and eventually coming back to the starting point. In this case, such paths are called “Hamiltonian cycles” and have been enumerated and classified (Albini and Antonini 2009) according to their inner symmetries. There are in fact Hamiltonian cycles which are “redundant” (meaning that they are generated by the repetition of a given pattern) and other cycles which are “maximal” (meaning that they are not obtained as a concatenation of a same pattern of P, L and/or R transformations). Such maximal Hamiltonian cycles have been used by one of the authors in the instrumental parts of the song *Aprile,* inspired by a text from the Italian decadent poet Gabriele D’Annunzio (1863–1938). More precisely, three structurally different Hamiltonian cycles have been used, with the goal of systematically frustrating the

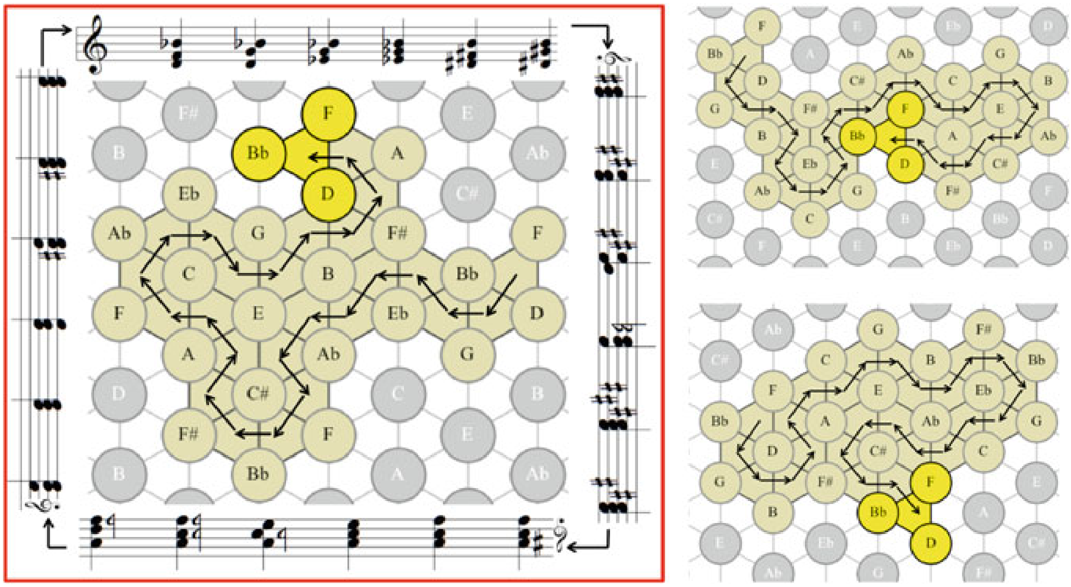


Fig. 7 The three maximal Hamiltonian cycles used in the instrumental part of the song *Aprile* by Moreno Andreatta, inspired by a Gabriele D'Annunzio poem (1863–1938)

expectation of the listener, whose perception cannot find the logic in the three selected progressions of chords (Fig. 7).[12]

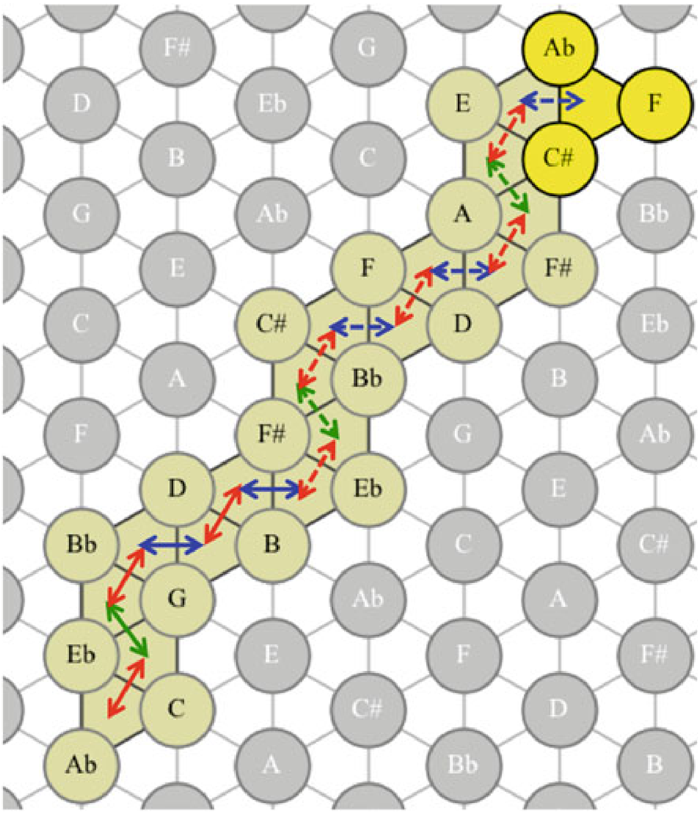
The previous example shows the interest of using Hamiltonian properties of chord progressions in a popular music context. Despite their intriguing character, Hamiltonian cycles are challenging objects for music perception and cognition. One may question their capability of providing harmonic material that the musical mind can process, without getting lost in the underlying maximal variety principle.[13] Since evidences of the perceptual relevance of these geometric and combinatorial structures are still lacking, it seems reasonable to try to add some inner symmetries in the Hamiltonian cycles used in song writing. Redundancy in the inner structure of the Hamiltonian harmonic progressions has been used by one of the authors (Moreno Andreatta) in the song entitled *La sera non è più la tua canzone* and based on a poem by Mario Luzi (1914–2005). Hamiltonian cycles are not only used in the instrumental parts, but—more challenging—in the verse, which obliges to create a melody capable of supporting a continuously changing harmony. Due to its inner

---

[12] The Hamiltonian trajectories of the song have been visualised by Gilles Baroin by mixing his *Hypersphere of Chords* representation and the traditional *Tonnetz*. It is available online at the address: (www.mathemusic.net).

[13] Note that "hamiltonicity" does not only concern popular music strategies, but it plays an important role in contemporary art music. The history of Twentieth-Century music shows that Hamiltonian properties have been implicitly used by composers such as Pierre Boulez or Milton Babbitt, who developed combinatorial strategies as natural extensions of the twelve-tone compositional system. Both composers and music theorists claimed the necessity of having a "maximal variety principles" in composition, in order to precisely question the notion of expectation in the musical listening process.

Fig. 8 The redundant Hamiltonian cycle used in the song *La sera non è più la tua canzone* (music by Moreno Andreatta, based on a poem by Mario Luzi)



symmetry, the cycle of length 24 is obtained by repeating four times the pattern LRLPLP of six transformations, as shown in Fig. 8.

The Fig. 9 shows the visualisation of the redundant Hamiltonian cycle utilized in the song *La sera non è più la tua canzone* in a new *Tonnetz* representation called the *Spinnen-Tonnetz*.

Although one of the main features of the *Spinnen-Tonnetz* is to provide a tonal centre to a harmonic progression, hamiltonicity makes the recognition of a tonality impossible in the case of the previous song. This fact opens interesting questions about the capability, for the musical mind to grasp these mathematical representations and to follow the logics of continuous modulations. One of the objectives of the “Math’n Pop” project, which is carried on within the GDR ESARS, is precisely to go deeper into the connections between cognitive neurosciences and algebraic/geometric formalisations of musical structures and processes. As shown by Zatorre and Krumhansl (2002), the mental key maps are related to the way in which a major (resp. minor) chord is surrounded by minor (resp. major) chords having two notes in common. Although the authors do not make any reference to the neo-Riemannian transformations, the geometric space they suggest to use is precisely the traditional *Tonnetz*.[14]

---

[14] We analysed the relations between mental and mathematical representations of music in Acotto and Andreatta (2012).

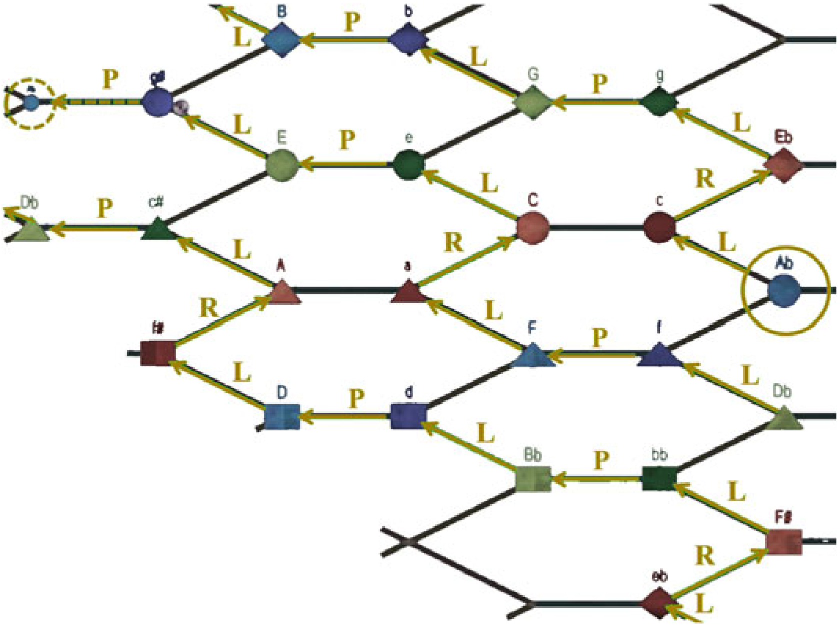


Fig. 9 The visualisation of the trajectory corresponding to the redundant Hamiltonian cycle used in the song *La sera non è più la tua canzone* in the *Spinnen-Tonnetz*. The *circle* shows the initial chord of the Hamiltonian progression (which—because of the cyclic character of the path—is the same as the final chord, indicated with a *dotted circle*)

Conclusions and Perspectives for Future Research

Starting from the analytical examples presented in this paper, together with the compositional applications that we have briefly sketched, it is clear that the popular music repertoire (including pop music, jazz, rock and *chanson*) can largely benefit from the use of formal and computational models. Although we have focused our attention on symbolic approaches and, in particular, on algebraic and geometric models, one interesting research area is precisely the interaction between symbolic approaches and different techniques based on signal processing within the field of Music Information Retrieval (MIR). A first attempt at filling the gap between these two main components of MIR has been carried on by using dissonance functions and advanced tools in algebraic topology in order to deform the original *Tonnetz* into an anisotropic structure (Bergomi and Andreatta 2015; Bergomi 2015; Bergomi et al. 2015). An example of deformation of the vertices of the *Tonnetz*

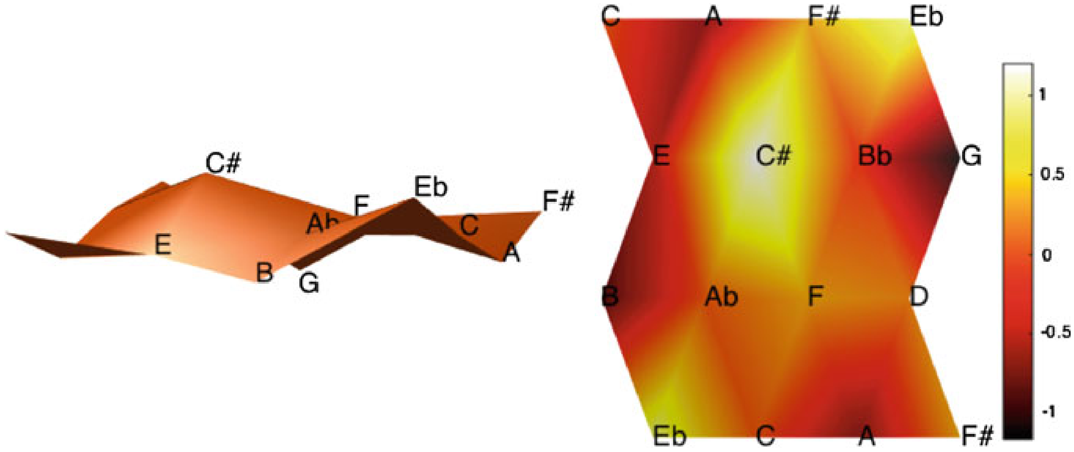


Fig. 10 The anisotropic *Tonnetz* whose vertices are deformed by a dissonance function (in this special case it is the dissonance induced by a C major chord. The figure is taken from Bergomi and Andreatta 2015)

leading to an anisotropic geometric space is shown in Fig. 10. This new structure might be an excellent case study in order to fill the gap between the computational musicological community and the neuroscientists working on the cognitive aspects of the geometric formalisations of musical structures and processes.[15]

References

Acotto E, Andreatta M (2012) Between mind and mathematics. Different kinds of computational representations of music. Math Soc Sci 199:9–26

Agon C (2004). Langages de programmation pour la composition musicale. Habilitation à Diriger des Recherches, Université de Paris 6

Albini G, Antonini S (2009) Hamiltonian cycles in the topological dual of the Tonnetz. In: Proceedings of the Yale MCM conference, Springer, LNCS

Andreatta M (2010) Mathematica est exercitium musicae. La recherche 'mathémusicale' et ses interactions avec les autres disciplines, Habilitation à Diriger des Recherches, IRMA/Université de Strasbourg

Andreatta M (2014a) Modèles formels dans et pour la musique pop, le jazz et la chanson: introduction et perspectives futures. In: Kapoula Z, Lestocart L-J, Allouche J-P (eds) Esthétique & Complexité II: Neurosciences, évolution, épistémologie, philosophie, éditions du CNRS, pp 69–88

Andreatta M (2014b) Math'n pop: géométrie et symétrie eu service de la chanson. Tangente. L'aventure mathématique, special issue devoted on the creative process in mathematics, pp 92–97

Andreatta M (2016) Musique savante/musiques actuelles: articulations, special issue of the journal *Musimédiane*, French Society of Music Analysis

---

[15] A special issue of the *Journal of Mathematics and Music* has been devoted to this specific problem with precisely the aim of bridging the Gap between Computational/Mathematical and Cognitive Approaches in Music Research. See Volk and Honingh (2002).

Andreatta M, Ehresmann A, Guitart R, Mazzola G (2013) Towards a categorical theory of creativity. In: Yust J et al. (eds) Proceedings of the mathematics and computation in music conference 2013—Springer, Lecture notes in computer science, vol 7937

Baroin G (2011) The planet-4D model: an original hypersymmetric music space based on graph theory. In: Agon C, Andreatta M, Assayag G, Amiot E, Bresson J, Mandereau J (eds) Proceedings of the mathematics and computation in music conference 2011, Springer, Lecture notes in computer science, vol 6726, pp 326–329

Bergomi M (2015) Dynamical systems and musical structures, PhD, UPMC/LIM Milan/IRCAM

Bergomi M, Andreatta M (2015) Math'n pop versus Math'n folk? A computational (ethno)-musicological approach. In: Proceedings international folk music analysis conference, Paris, pp 32–34

Bergomi M, Fabbri F, Andreatta M (2015) Hey maths! Modèles formels et computationnels au service des Beatles. Volume! La revue des musiques populaires (eds by Grégoire Tosser and Olivier Julien, special issue devoted to the Beatles)

Bigo L (2013) Représentations symboliques musicales et calcul spatial, PhD, University of Paris Est/IRCAM

Bigo L, Andreatta M (2014) A geometrical model for the analysis of pop music. Sonus 35(1):36–48

Bigo L, Andreatta M (2015) Topological structures in computer-aided music analysis. In: Meredith D (ed) Computational music analysisy. Springer, pp 57–80

Bigo L, Andreatta M, Giavitto J-L, Michel O, Spicher A (2013) Computation and visualization of musical structures in chord-based simplicial complexes. In: Yust J et al (eds) Proceedings of the mathematics and computation in music conference 2013, Springer, lecture notes in computer science, vol 7937, pp 38–51

Boulez P, Connes A (2011) Creativity in mathematics and music. Mathematics and computation in music conference, IRCAM. Video available online at the address http://agora2011.ircam.fr

Briginshaw S (2012) A neo-riemannian approach to jazz analysis. Nota Bene Can Undergraduate J Musicol 5(1, Article 5). Available online at http://ir.lib.uwo.ca/notabene/vol5/iss1/5

Capuzzo G (2004) Neo-Riemannian theory and the analysis of pop-rock music. Music Theory Spectrum 26(2):177–199

Connes A (2004) CNRS images, Vidéothèque du CNRS, 2004. Available online at http://videotheque.cnrs.fr/

Cohn R (2012) Audacious euphony: chromatic harmony and the triad's second nature. Oxford University Press

Euler L (1774) De harmoniae veris principiis per speculum musicum repraesentatis. In: Novi Commentarii academiae scientiarum Petropolitanae 18:330–353

Gollin E, Rehding A (2014) The Oxford handbook of Neo-Riemannian music theories. Oxford

Hascher X, Papadopoulos A (2015) Leonhard Euler. Mathématicien, physicien et théoricien de la musique, CNRS éditions

Hascher X (2007) A harmonic investigation into three songs of the beach boys: *all summer long, help me Rhonda, California Girls*. SONUS 27(2):27–52

Lewin D (1987/2007) Generalized musical intervals and transformations. Yale University Press (orig. Yale University Press. Reprint Oxford University Press, 2007)

Lewin D (1993/2007) Musical form and transformation. Yale University Press (orig. Yale University Press. Reprint Oxford University Press, 2007)

Mersenne M (1636) Harmonie universelle, contenant la théorie et la pratique de la musique. Paris

Seress H, Baroin G (2016) Le *Tonnetz* en musique savante et en musique populaire. In: Andreatta M (ed) Musique savante/musiques actuelles: articulations, *Musimédiane* (forthcoming)

Tagg PH (1982) Analysing popular music: theory, method and practice. Popular Music 2:37–67

Volk A, Honingh A (2002) Mathematical and computational approaches to music: three methodological reflections. Spec Issue J Math Music 6(2)

Zatorre RJ, Krumhansl CL (2002) Mental models and musical minds. Science 298(5601):2138–2139. (13 December)

The Evolution of Aesthetics: A Review of Models

Julien P. Renoult

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 of "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.

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

---

J.P. Renoult (✉)
Institute of Arts Creations Theories and Aesthetics, CNRS-University Paris 1 Panthéon, Sorbonne, 47 r. des bergers, 75015 Paris, France
e-mail: jurenoult@gmail.com

Z. Kapoula and M. Vernet (eds.), *Aesthetics and Neuroscience*,
DOI 10.1007/978-3-319-46233-2_17

mechanisms underlying the aesthetic experience.[1] 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 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 out 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 starring 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 seem 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 (Polyommatinae), 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.

---

[1] 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.

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.[2]

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.

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)

---

[2] 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 valuated stimulus.

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 highest aesthetic merit for 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 it 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 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 a 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.

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, 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.

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.[3]

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 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

---

[3] 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.

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 any, 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 that can 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 loose 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.

Fisher's Model of Aesthetic Preferences

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.

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 the misinterpretation of Darwin's original view of sexual selection is.

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, pp. 39, 233). But Darwin was explicit that the "taste for 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 aesthetical. 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 aesthetical.

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 proteiformous 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.

Exploitative Beauty

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 (Birkhoff 1933). 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 describe 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 h 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.[4] 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.

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 2007). 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.

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

---

[4] 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.

information efficiently, notably by removing the many redundancies that occur in natural stimuli (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 evidences that stimuli mimicking the redundancies in visual representations of nature are more efficiently processed by the visual system, which increases their aesthetic appeal (Redies 2007; 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 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".

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 revaluate 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 et al. (2012) demonstrated this by showing that people tend to prefer photos of flying eagles and of swimming sting rays where eagles and rays where placed at the top and at the bottom of images, respectively.

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. 2016a, b). 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 2.5–3.5 % 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.

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 as 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[5] 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 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

---

[5] 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.

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.

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.

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.

References

Appleton J (1975) The experience of landscape. Wiley, New York

Arak A, Enquist M (1993) Hidden preferences and the evolution of signals. Philos Trans R Soc Lond B 340:207–213

Arnold SJ, Pfrender ME, Jones AG (2001) The adaptive landscape as a conceptual bridge between micro- and macroevolution. Genetica 112:9–32

Attwell D, Laughlin SB (2001) An energy budget for signaling in the grey matter of the brain. J Cereb Blood Flow Metab 21(10):1133–1145

Bailey WB, Moore AJ (2012) Runaway sexual selection without genetic correlations: social environments and flexible mate choice initiate and enhance the Fisher process. Evolution 66 (9):2674–2684

Balling JD, Falk JH (1982) Development of visual preference for natural environments. Environ Behav 14(1):5–28

Barkow JH, Cosmides L, Tooby J (1995) The adapted mind: evolutionary psychology and the generation of culture. Oxford University Press

Barlow H (1961) Possible principles underlying the transformations of sensory messages. In: Rosenblith W (ed) Sensory communication. MIT Press, Cambridge

Barlow H (2001) Redundancy reduction revisited. Netw Comput Neural Syst 12(3):241–253

Berridge KC, Kringelbach ML (2008) Affective neuroscience of pleasure: reward in humans and animals. Psychopharmacology 199(3):457–480

Berridge KC, Robinson TE, Aldridge JW (2009) Dissecting components of reward: ‘liking’, ‘wanting’, and learning. Curr Opininion Pharmacol 9(1):65–73

Birkhoff GD (1933) Aesthetic measure. Harvard University Press, MA, USA

Bornstein RF (1989) Exposure and affect: overview and meta-analysis of research, 1968–1987. Psychol Bull 106(2):265–289

Bowmaker JK, Govardovskii VI, Shukolyukov SA, Zueva JL, Hunt DM, Sideleva VG, Smirnova OG (1994) Visual pigments and the photic environment: the cottoid fish of Lake Baikal. Vision Res 34(5):591–605

Bradley MM (2009) Natural selective attention: orienting and emotion. Psychophysiology 46 (1):1–11

Bruce LL, Neary TJ (1995) The limbic system of tetrapods: a comparative analysis of cortical and amygdalar populations. Brain Behav Evol 46(4–5):224–234

Buchsbaum G, Gottschalk A (1983) Trichromacy, opponent colour coding and optimum colour information transmission in the retina. Proc R Soc Lond Biol Sci 220:89–113

Burrows H (2013) Biological actions of sex hormones. Cambridge University Press

Buss DM (1989) Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. Behav Brain Sci 12(01):1–14

Carleton KL (2009) Cichlid fish visual systems: mechanisms of spectral tuning. Integr Zool 4 (1):75–86

Chatterjee A (2003) Prospect for a cognitive neuroscienceof visual aesthetics. Bull Psychol Arts 4:55–60

Chatterjee A (2013) The aesthetic brain: how we evolved to desire beauty and enjoy art. Oxford University Press, USA

Child IL, Siroto L (1965) Bakwele and American esthetic evaluations compared. Ethnology 4:349–360

Clara E, Regolin L, Vallortigara G (2007) Preference for symmetry is experience dependent in newborn chicks (*Gallus gallus*). J Exp Psychol 33(1):12–20

Clemens J, Kutzki O, Ronacher B, Schreiber S, Wohlgemuth S (2011) Efficient transformation of an auditory population code in a small sensory system. Proceedings of the National Academy of Sciences of the USA 108(33):13812–13817

Clore GL, Wyer RS Jr, Dienes B, Gasper K, Gohm C, Isbell L (2001) Affective feelings as feedback: some cognitive consequences. In: Martin LL, Clore GL (eds) Theories of mood and cognition: a user's guidebook. Lawrence Erlbaum Associates Publishers, Mahwah, NJ, pp 27–62

Coeterier JF (1996) Dominant attributes in the perception and evaluation of the Dutch landscape. Landscape Urban Plann 34(1):27–44

Cohen J (1964) Dependency of the spectral reflectance curves of the munsell-color chips. Psychon Sci 1(12):369–370

Cosmides L, Tooby J (1987) From evolution to behavior: evolutionary psychology as the missing link. In: Dupre J (ed) The latest on the best: essays on evolution and optimality. MIT Press, Cambridge, MA, pp 277–306

Cotton S, Fowler K, Pomiankowski A (2004) Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? Proc R Soc Lond B Biol Sci 271:771–783

Cronin H (1991) The ant and the peacock. Cambridge University Press, Cambridge

Cummings M, Partridge J (2001) Visual pigments and optical habitats of surfperch (Embiotocidae) in the California kelp forest. J Comp Physiol A 187(11):875–889

Cummings ME (2007) Sensory trade-offs predict signal divergence in surfperch. Evolution 61:530–545

Danchin É, Giraldeau L-A, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. Science 305(5683):487–491

Darwin C (1859) On the origins of species by means of natural selection. John Murray, London

Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London

Darwin C (1872) The expression of the emotions in man and animals. John Murray, London

Dongen SV (2006) Fluctuating asymmetry and developmental instability in evolutionary biology: past, present and future. J Evol Biol 19(6):1727–1743

Ekman P (1992) An argument for basic emotions. Cogn Emot 6(3–4):169–200

Endler JA, Basolo AL (1998) Sensory ecology, receiver biases and sexual selection. Trends Ecol Evol 13(10):415–420

Enquist M, Arak A (1994) Symmetry, beauty and evolution. Nature 372:169–172

Fantz RL (1957) Form preferences in newly hatched chicks. J Comp Physiol Psychol 50(5):422

Farkas A (2002) Prototypicality-effect in surrealist paintings. Empirical Stud Arts 20:127–136

Field DJ (1987) Relations between the statistics of natural images and the response proporties of cortical cells. J Opt Soc Am A 4:2379–2394

Fisher RA (1915) The evolution of sexual preference. Eugenics Rev 7:184–191

Folstad I, Karter AJ (1992) Parasites, bright males, and the immuno-completence handicap. Am Nat 139:603–622

Friston K, Kiebel S (2009) Predictive coding under the free-energy principle. Philos Trans R Soc Lond B Biol Sci 364(1521):1211–1221

Garcia CM, Ramirez E (2005) Evidence that sensory traps can evolove into honest signals. Nature 434:501–505

Garner WR, Clement DE (1963) Goodness of pattern and pattern uncertainty. J Verbal Learn Verbal Behav 2(5):446–452

Getty T (2006) Sexually selected signals are not similar to sports handicaps. Trends Ecol Evol 21:83–88

Ghirlanda S, Jansson L, Enquist M (2002) Chickens prefer beautiful humans. Human Nat 13 (3):383–389

Graham DJ, Field DJ (2007) Statistical regularities of art images and natural scenes: spectra, sparseness and nonlinearities. Spat Vis 21(1):149–164

Graham DJ, Redies C (2010a) Statistical regularities in art: relations with visual coding and perception. Vision Res 50(16):1503–1509

Graham DJ, Redies C (2010b) Statistical regularities in art: relations with visual coding and perception. Vision Res 50(16):1503–1509

Grammer K, Fink B, Møller AP, Thornhill R (2003) Darwinian aesthetics: sexual selection and the biology of beauty. Biol Rev 78(3):385–407

Grammer K, Thornhill R (1994) Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. J Comp Psychol 108(3):233–242

Grose J (2011) Modelling and the fall and rise of the handicap principle. Biol Philos 26(5):677–696

Hald A (1998) A history of mathematical statistics. Wiley, NY

Han K-T (2007) Responses to six major biomes in terms of scenic beauty, preference, and restorativeness. Environ Behav 39:529–556

Iwao S, Child IL, García M (1969) Further evidence of agreement between Japanese and American esthetic evaluations. J Soc Psychol 78(1):11–15

Jacobsen T, Hofel LEA (2002) Aesthetic judgments of novel graphic patterns: analyses of individual judgments. Percept Motor Skills 95(3):755–766

Jones D, Hill K (1993) Criteria of facial attractiveness in five populations. Human Nat 4(3):271–296

Kant I (1790/1987) Critique of Judgment, W. S. Pluhar (transl.). Hackett, Indianapolis

Kaplan R, Kaplan S (1989) The experience of nature: a psychological perspective. Cambridge University Press, New York

Kirkpatrick M (1982) Sexual selection and the evolution of female choice. Evolution 36:1–12

Kirkpatrick M, Ryan M (1991) The paradox of the lek and the evolution of mating preferences. Nature 350:33–38

Kokko H, Brooks R, Jennions MD, Morley J (2003) The evolution of mate choice and mating biases. Proc R Soc Lond B 270:653–664

Kreutzer M, Aebischer V (2015) The riddle of attractiveness: looking for an 'Aesthetic Sense' within the hedonic mind of the beholders. In: Current perspectives on sexual selection. Springer, pp 263–287

Kuo FE, Bacaicoa M, Sullivan WC (1998) Transforming inner-city landscapes trees, sense of safety, and preference. Environ Behav 30(1):28–59

Lande R (1981) Models of speciation by sexual selection on polygenic traits. Proc Nat Acad Sci USA 78:3721–3725

Langlois JH, Ritter JM, Roggman LA, Vaughn LS (1991) Facial diversity and infant preferences for attractive faces. Dev Psychol 27(1):79

Langlois JH, Roggman LA (1990) Attractive faces are only average. Psychol Sci 1(2):115–121

Laughlin SB (2001) Energy as a constraint on the coding and processing of sensory information. Curr Opin Neurobiol 11(4):475–480

Law-Smith MJ, Perrett DI, Jones BC, Cornwell RE, Moore FR, Feinberg DR, Boothroyd LG, Durrani SJ, Stirrat MR, Whiten S (2006) Facial appearance is a cue to oestrogen levels in women. Proc R Soc Lond B Biol Sci 273(1583):135–140

Lennie P (2003) The cost of cortical computation. Curr Biol 13(6):493–497

Liang J, Shang Y (2013) Estrogen and cancer. Annu Rev Physiol 75:225–240

Lie HC, Rhodes G, Simmons LW (2008) Genetic diversity revealed in human faces. Evolution 62 (10):2473–2486

Light LL, Hollander S, Kayra-Stuart F (1981) Why attractive people are harder to remember. Pers Soc Psychol Bull 7(2):269–276

Lin S, Owald D, Chandra V, Talbot C, Huetteroth W, Waddell S (2014) Neural correlates of water reward in thirsty *Drosophila*. Nat Neurosci 17:1536–1542

Mather G (2014) The psychology of visual art: eye, brain and art. Cambridge University Press, Cambridge, UK

Maynard-Smith J, Harper DGC (1995) Animal signals: models and terminology. J Theor Biol 177:305–311

Møller AP (1992) Parasites differentially increase the degree of fluctuating asymmetry in secondary sexual characteristics. J Evol Biol 5:691–699

Møller AP, Sorci G (1998) Insect preference for symmetrical artificial flowers. Oecologia 114 (1):37–42

Morris MR (1998) Female preference for trait symmetry in addition to trait size in swordtail fish. Proc R Soc Lond B Biol Sci 265(1399):907–907

Olshausen BA, Field DJ (2004) Sparse coding of sensory inputs. Curr Opin Neurobiol 14:481–487

Orians GH, Heerwagen JH (1992) Evolved responses to landscapes. In: Barkow JH, Cosmides L, Tooby J (eds) The adapted mind: evolutionary psychology and the generation of culture. Oxford University Press, New York, NY, pp 555–579

Palm G (2013) Neural associative memories and sparse coding. Neural Netw 37:165–171

Palmer AR, Strobeck C (1986) Fluctuating asymmetry: measurement, analysis, patterns. Annu Rev Ecol Syst 17:391–421

Palmer SE, Griscom WS (2013) Accounting for taste: individual differences in preference for harmony. Psychon Bull Rev 20(3):453–461

Palmer SE, Schloss KB, Sammartino J (2012) Hidden knowledge in aesthetic judgments. In: Shimada H, Palmer SE (eds) Aesthetic science—connecting minds, brains, and experience. Oxford University Press, New-York, NY

Palmer SE, Schloss KB, Sammartino J (2013) Visual aesthetics and human preference. Annu Rev Psychol 64:77–107

Parsons PA (1990) Fluctuating asymmetry: an epigenetic measure of stress. Biol Rev 65(2):131–145

Penton-Voak IS, Chen JY (2004) High salivary testosterone is linked to masculine male facial appearance in humans. Evol Human Behav 25(4):229–241

Pérez-Rodríguez L, Jovani R, Mougeot F (2013) Fractal geometry of a complex plumage trait reveals bird's quality. Proc R Soc Lond B Biol Sci 280(1755):20122783

Pisanski K, Feinberg DR (2013) Cross-cultural variation in mate preferences for averageness, symmetry, body size, and masculinity. Cross Cult Res 47(2):162–197

Polak M, Møller AP, Gangestad SW, Kroeger DE, Manning JT, Thornhill R (2003) Does an individual asymmetry parameter exist? A meta-analysis. In: Polak M(ed) Developmental instability: causes and consequences. Oxford University Press, Oxford

Prum RO (2010) The Land-Kirkpatrick mechanism is the null model of evolution by intersexual selection: implications for meaning, honesty, and design in intersexual signals. Evolution 64:3085–3100

Prum RO (2012) Aesthetic evolution by mate choice: Darwin's *really* dangerous idea. Philos Trans R Soc B Biol Sci 367:2253–2265

Prum RO (2013) Coevolutionary aesthetics in human and biotic artworlds. Biol Philos 28:811–832

Rao RPN, Ballard DH (1999) Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nat Neurosci 2(1):79–87

Reber R (2012) Processing fluency, aesthetic pleasure, and culturally shared taste. In: Shimamura AP, Palmer SE (eds) Aesthetic science, connecting minds, brains, and experience. Oxford University Press, NY

Reber R, Schwarz N (2006) Perceptual fluency, preference, and evolution. Polish Psychol Bull 1 (37):16–22

Reber R, Schwarz N, Winkielman P (2004) Processing fluency and aesthetic pleasure: is beauty in the perceiver's processing experience? Pers Soc Psychol Rev 8:364–382

Reber R, Winkielman P, Schwarz N (1998) Effects of perceptual fluency on affective judgments. Psychol Sci 9(1):45–48

Redies C (2007) A universal model of esthetic perception based on the sensory coding of natural stimuli. Spat Vis 21(1):97–117

Redies C (2015) Combining universal beauty and cultural context in a unifying model of visual aeshtetic experience Fontiers in Human. Neuroscience 9:218

Redies C, Brachmann A, Hayn-Leichsenring GU (2015) Changes of statistical properties during the creation of graphic artworks. Art Percept 3(1):93–116

Redies C, Hänisch J, Blickhan M, Denzler J (2007a) Artists portray human faces with the Fourier statistics of complex natural scenes. Netw Comput Neural Syst 18(3):235–248

Redies C, Hasenstein J, Denzler J (2007b) Fractal-like image statistics in visual art: similarity to natural scences. Spat Vis 21:137–148

Renoult JP, Bovet J, Raymond M (2016a) Beauty is in the efficient coding of the beholder. R Soc Open Sci. doi:10.1098/rsos.160027

Renoult JP, Kelber A, Schaefer HM (2016) Colour spaces in ecology and evolution. Biol Rev (in press). doi:10.1111/brv.12230

Rhodes G (2006) The evolutionary psychology of facial beauty. Annu Rev Psychol 57:199–226

Rhodes G, Sumich A, Byatt G (1999) Are average facial configurations attractive only because of their symmetry? Psychol Sci 10(1):52–58

Rhodes G, Yoshikawa S, Palermo R, Simmons LW, Peters M, Lee K, Halberstadt J, Crawford JR (2007) Perceived health contributes to the attractiveness of facial symmetry, averageness, and sexual dimorphism. Perception 36:1244–1252

Robinson TE, Berridge KC (2008) The incentive sensitization theory of addiction: some current issues. Philos Trans R Soc B Biol Sci 363(1507):3137–3146

Rodríguez I, Gumbert A, de Ibarra NH, Kunze J, Giurfa M (2004) Symmetry is in the eye of the 'beeholder': innate preference for bilateral symmetry in flower-naïve bumblebees. Naturwissenschaften 91(8):374–377

Rosch E (1975) Cognitive representations of semantic categories. J Exp Psychol 104(3):192

Ruso B, Renninger LA, Atzwanger K (2003) Human habitat preferences: a generative territory for evolutionary aesthetics research. In: Voland E, Grammer K (eds) Evolutionary aesthetics. Springer-Verlag, Berlin, pp 279–294

Ryan MJ, Cummings ME (2013) Perceptual biases and mate choice. Annu Rev Ecol Evol 44:437–459

Ryan MJ, Fox JH, Wilczynski W, Rand AS (1990) Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. Nature 343(6253):66–67

Ryan MJ, Rand A (1993) Sexual selection and signal evolution: the ghost of biases past. Philos Trans R Soc Lond B 340:187–195

Schaefer HM, Ruxton G (2015) Signal diversity, sexual selection, and speciation. Annu Rev Ecol Evol Syst 46:573–592

Schaefer HM, Ruxton GD (2009) Deception in plants: mimicry or perceptual exploitation? Trends Ecol Evol 24:676–685

Schwarz N (1990) Feelings as information: informational and motivational functions of affective states. In: Higgins ET, Sorrentino RM, Richard M (eds) Handbook of motivation and cognition: foundations of social behavior, vol 2. Guilford Press, New York, pp 527–561

Shimamura AP, Palmer SE (2012) Aesthetic science: connecting minds, brains, and experience. Oxford University Press, New York

Silvia PJ, Barona CM (2009) Do people prefer curved objects? Angularity, expertise, and aesthetic preference. Empirical Stud Arts 27(1):25–42

Simoncelli EP (2003) Vision and the statistics of the visual environment. Curr Opin Neurobiol 13 (2):144–149

Simoncelli EP, Olshausen BA (2001) Natural image statistics and neural representation. Annu Rev Neurosci 24:1193–1216

Skamel U (2003) Beauty and sex appeal: sexual selection of aesthetic preferences. In: Voland E, Grammer K (eds) Evolutionary aesthetics. Springer-Verlag, Berlin

Spaethe J, Tautz J, Chittka L (2001) Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. Proc Nat Acad Sci USA 98(7):3898–3903

Stevens M (2013) Sensory ecology, evolution, & behaviour. Oxford University Press

Swaddle JP, Cuthill IC (1994) Preference for symmetric males by female zebra finches. Nature 367:165–166

Számado S (2011) The cost of honesty and the fallacy of the handicap principle. Anim Behav 81:3–10

ten Cate C, Rowe C (2007) Biases in signal evolution: learning makes a difference. Trends Ecol Evol 22:380–387

Thornhill R (2003) Darwinian aesthetics informs traditional aesthetics. In: Voland E, Grammer K (eds) Evolutionary aesthetics. Springer-Verlag, Berlin Heidelberg, pp 9–35

Thornhill R, Grammer K (1999) The body and face of woman: one ornament that signals quality? Evol Human Behav 20(2):105–120

Topolinski S, Erle TM, Reber R (2015) Necker's smile: immediate affective consequences of early perceptual processes. Cognition 140:1–13

Trehub SE (2000) Human processing predispositions and musical universals. In: Wallin NL, Brown S, Merker B (eds) The origins of music. MIT Press, Cambridge, USA, pp 427–448

Ulrich RS (1981) Natural versus urban spaces: some psycholphysiological effects. Environ Behav 13:523–556

Valentine CW (1962) The experimental psychology of beauty. Methuen, London

Wallace AR (1895) Natural selection and tropical nature, 2nd. MacMillan and Co, New York, NY

Whitfield TWA, Slatter PE (1979) The effects of categorization and prototypicality on aesthetic choice in a furniture selection task. Br J Psychol 70(1):65–75

Willshaw DJ, Buneman OP, Longuet-Higgins HC (1969) Non-holographic associative memory. Nature 222:960–962

Winkielman P, Cacioppo JT (2001) Mind at ease puts a smile on the face: psychophysiological evidence that processing facilitation elicits positive affect. J Pers Soc Psychol 81(6):989

Winkielman P, Halberstadt J, Fazendeiro T, Catty S (2006) Prototypes are attractive because they are easy on the mind. Psychol Sci 17(9):799–806

Winkielman P, Schwarz N, Fazendeiro T, Reber R (2003) The hedonic marking of processing fluency: Implications for evaluative judgment. In: Musch J, Klauer KC (eds) The psychology of evaluation: affective processes in cognition and emotion. Psychology Press, pp 189–217

Zahavi A (1975) Mate selection: a selection for a handicap. J Theor Biol 53:204–214

Zahavi A, Zahavi A (1997) The handicap principle. Oxford University Press, Oxford

Zajonc RB (1968) Attitudinal effects of mere exposure. J Pers Soc Psychol 9(2p2):1–27

Zaslaver A, Liani I, Shtangel O, Ginzburg S, Yee L, Sternberg PW (2015) Hierarchical sparse coding in the sensory system of *Caenorhabditis elegans*. Proc Nat Acad Sci USA 201423656

Zebrowitz LA, Montepare JM, Lee HK (1993) They don't all look alike: individual impressions of other racial groups. J Pers Soc Psychol 65(1):85

Zebrowitz LA, Wang R, Bronstad PM, Eisenberg D, Undurraga E, Reyes-García V, Godoy R (2012) First impressions from faces among US and culturally isolated Tsimane'people in the Bolivian rainforest. J Cross Cult Psychol 43(1):119–134

Philosophical Aesthetics and Neuroaesthetics: A Common Future?

Bruno Trentini

Abstract The future of the art/science relationship does not only concern the field of artistic creation, but also the field of aesthetic experience. In fact, whereas aesthetics has existed as a philosophical discipline since the 18th century, more and more scientific experimental works study aesthetic experience. Philosophical aesthetics now shares its object of study with what is often called neuroaesthetics. The aim of this chapter is to shape a common vision enabling philosophical aesthetics and neuroaesthetics to pool their results and their tools so that the research world does not suffer from a regrettable scission in the field of theory of artistic theory. Indeed, aesthetics seems to have a lot to gain from physiological studies dealing, on the one hand, with the capacity of cognitive processes to adapt to non-routine situations and, on the other hand, with the capacity of these adaptations to be felt by individuals.

It does not seem possible to isolate cognitive processes that are specific to aesthetic experiences. For instance, perception processes are very frequently involved in the experience of a work of art, and are systematically involved in the reception of an anamorphosis by Felice Varini or an immersive work by Ann Veronica Janssens. Premotor and motor processes seem necessary to mentally reconstruct the poietic gesture in front of a work by Jackson Pollock, or to interact with a work by Maurice Benayoun. The list could go on and on. It would besides be very surprising to find a kind of cognitive process that works of art cannot activate and it is easy to think about works of art that each mobilizes many kinds of cognitive processes. The understanding of each process in isolation is not yet sufficient to understand what aesthetic experience is.

This chapter is the translation of my French paper: Trentini B (2015) Quelle naturalisation pour quelle esthétique? (Which Naturalization for Which Aesthetics? Nouvelle revue d'esthétique no 15:59–67.

B. Trentini (✉)
ACTE: Institute of Arts Creations Theories and Aesthetics,
CNRS and University Paris 1 Panthéon-Sorbonne, Paris, France
e-mail: b.trentini@laposte.net

Z. Kapoula and M. Vernet (eds.), *Aesthetics and Neuroscience*,
DOI 10.1007/978-3-319-46233-2_18

These observations highlight the fact that aesthetic experience is integrative, that is to say that it involves many levels of cognition, and that it cannot be reduced to an atomic behavior; in other words: it is complex. Regarding the issue of naturalization of aesthetics, this complexity can be interpreted in two different ways: either we consider that the aesthetician cannot dispense with the understanding of the cognitive processes involved in aesthetic experience, or we consider that any attempt at naturalization is detrimental to aesthetics, because the mere fact of trying to naturalize experiences that are so complex would inevitably lead to a harmful reduction of the field. Besides, regardless of whether naturalization is desirable or not, we can first wonder if this approach is even possible. Yet, if we define naturalization as a scientific approach aiming at finding observables that can give account for issues that were initially not related with physiology—that were not embodied—, the complexity of aesthetic experience makes it almost impossible to find relevant observables. This chapter notably aims at defining the observables which would be interesting to study in order to naturalize aesthetics. Of course, the choice of the observables and the choice of the concepts of philosophical aesthetics to be naturalized will impact the progression of the field: do we aim at naturalizing an aesthetic category like the beautiful or the sublime, or at naturalizing the specificity of any aesthetic experience? Of course, various possibilities exist and the mere fact of making a choice will necessarily tend to freeze and narrow the field down. However, in order to undertake the most relevant naturalization, it would be better if the naturalization of aesthetic experience did not shift the key issues of the field. As a consequence, the question of knowing if naturalization is desirable and the question of knowing if it is possible can be dealt with together. We should besides not forget that aesthetics was at the origin anchored in a physiological and even a psychophysical framework, and that contemporary aesthetics has developed from this framework of scientific naturalism. If the question of naturalization is now once again taking center stage, it is above all as a result of the emergence of cognitive science, which have modified the way we comprehend the relationship between human beings and their environment. Cognitive science notably enable us to think about sensitivity and intelligibility in another way, to think about the relationships between these two notions, and even to think without using these labels that arbitrarily create a distinction where maybe none is required. One main difficulty of the aesthetician indeed lies in the articulation of sensation and knowledge, perception and intellection.

Since naturalist investigations are de facto being carried out, the most important point to tackle the issue of the naturalization of aesthetics seems to be to figure out which naturalization is possible for the aesthetics that we wish. Thus, this chapter is intended both for the supporters of naturalization and for its firmest opponents, both for philosophers and for scientists. If choosing a specific label for the aesthetics proposed in this chapter was required, embodied aesthetics would best fit. Embodied aesthetics is the extension of embodied cognition, a philosophical trend proposed by Francisco Varela notably following the reading of the phenomenology of Merleau-Ponty: sensations, perceptions but also body and physiology are thus thought to be the main actors of aesthetic experience.

The first part of this article provides a presentation of the main experimental and epistemological pitfalls encountered in neuroaesthetical studies on the beautiful and pleasure. Not only is the study of the beautiful cut off from a considerable part of the artistic reality—which could be a conjectural and accidental problem—but it also presents difficulties that are not encountered in the study of the other aesthetic category defined in the 18th century, the sublime. The second part of this article puts emphasis on the sublime, showing that even though very few neuroaestheticians have worked on it until now, its naturalization is far more advanced. One of the best advantages of the sublime is that it involves cognitive processes that are quite well understood or at least much studied. We will finally discuss the resulting question of knowing whether it would be better to naturalize aesthetics or to encourage philosophical aestheticians to seize naturalized studies which do not necessarily deal with aesthetics.

Naturalization of the Experience of the Beautiful: Methodological and Epistemological Pitfalls

Even if the first studies carried out by Plato and Aristotle about artistic creation did not tackle the question of art by focusing on the beautiful but by focusing on imitation, the beautiful has prevailed as an artistic value, to such an extent that Hegel defined aesthetics as the science of fine art. If the beautiful has become the category which is the most (widely) studied by neuroaestheticians, this is of course because it is the most common and classical label. But this may also be because it seems easy to justify this aesthetic approach with respect to the Neo-Darwinist theories. For example, sexual attraction can be thought to be the substrate on which the beautiful has developed. Surprising as it may seem, this hypothesis was more or less already formulated in *The Symposium* by Plato, was put forward two millennia later by Nietzsche (Nietzsche 1889), and is nowadays defended by some researchers (Grammer et al. 2003). In other studies, a link between aesthetic experience and the prey/predator relationship is proposed (Smith 2005). These studies bet on a behavior that has increased the fitness of the individual. This hypothesis is deemed questionable since it explains aesthetic behavior only by the pleasure that is generated, without any consideration about the processes that generate this pleasure: according to Denis Dutton, this idea is as simplistic as thinking that a pleasure pill would be equivalent to aesthetic experience (Dutton 2009).

It is yet important not to confuse, on the one hand, the rooting of aesthetic behavior in the theory of evolution with, on the other hand, the naturalization of aesthetics, which consists in defining relevant observables. While the first is for the moment purely speculative, the second is an approach giving rise to practical experiments, which we can precisely discuss. There seems to be an epistemological problem which is inherent to the works dealing with the beautiful in art. This problem comes from the term “the beautiful” itself, which suffers from a strong socio-cultural bias. However, while he was aware of the subjectivity of the judgment of taste, the father of neuroaesthetics, Semir Zeki, chose to work on the beautiful. He is in that way consistent with a major philosophical tradition, since his more precise goal is to manage to naturalize the free play of faculties, which Kant supposed to be the major characteristic of the beautiful

(Kant 1790). Naturalization thus consists in finding an invariant that would systematically come into play when individuals feel a pleasure generated by an object that they find beautiful, and which would not or almost not hardly occur otherwise, in order to be able to *observe* the free play of faculties. Zeki searched for this invariant in cerebral activity, in a given cerebral area. In that sense, he assumed the existence of a "module"[1] of the beautiful. We will not discuss this hypothesis, but we will discuss some experiments aiming at testing it, more precisely the experiments described in the paper of Ishizu and Zeki (2011). It is worth noting that when Zeki and Ishizu studied individuals who are confronted with a work of art, they took care not to impose to the subjects an object that they, the experimenters, would found beautiful. They indeed asked the subjects to evaluate the beauty of the objects that were submitted on a scale from 1 to 9, in order to correct the bias due to differences in taste. Afterwards, Ishizu and Zeki tried to identify the specificity of the cerebral activity of the individuals while they were apprehending the objects that they, the subjects, had themselves judged as beautiful.

We cannot deny the fact that it is necessary in the design of the experiment to ask the individuals which objects they consider as beautiful, in order to take into account the taste of each of them. Nevertheless, this caution relies on a problematic introspection. Indeed, the beautiful that Zeki aimed at subjectively describing is very precise: the will of characterizing the neural bases of the experience of the beautiful presupposes the distinction between the beautiful and other positive categories like the agreeable or the sublime. Yet, the problem is that it is not wise to consider that the subjects who are studied by this neuroaesthetics are able to distinguish between these different positive aesthetic categories: many people use the term "beautiful" to characterize a rough ocean under a threatening sky, whereas they must activate cognitive processes that are very different from the ones they activate when they look at a "beautiful" bunch of tulips. This problem remains unaddressed by neuroaesthetics. The design of the experiments which focus on the beautiful does not usually take into account the different aesthetic categories (Cela-Conde et al. 2004, 2013; Zeki 1999)—and it will probably remain difficult to take these categories into account with non-expert subjects. It would thus be preferable to carry out experiments aiming at the naturalization of aesthetics without using a socio-cultural label as complicated as "beautiful". Unfortunately, asking for an introspection about aesthetic categories which are less used—and which are thus not mastered by everyone—would equally distort the results. The same criticism applies to the studies in which individuals are asked to classify works of art according to their aesthetic preferences (Vartanian and Goel 2004); the adjective "aesthetic" has had, in the everyday language, in English as well as in French, a meaning which is very different from the philosophical and neuroscientifical meaning which is supposed to be studied in these works. Thus, not only should not art be reduced to the beautiful, but another pitfall should also be avoided: aesthetic experience should not be reduced to pleasure. Even if we accept that all every aesthetic experience gives rise to pleasure, a major stake is to understand the

---

[1] This hypothesis is inspired by Jerry Fodor's research on the modularity of mind.

specificity of the pleasure of aesthetic experience. Once again, focusing on the category of the beautiful proves to be problematic: it wrongly suggests that, as soon as an aesthetic experience is unpleasant at any level, it cannot bring satisfaction. Some studies thus limit aesthetics to the beautiful, to the neutral and to the ugly (de Tommaso et al. 2008), or to an opposition between positive and negative values (Munar et al. 2012; Kreplin and Fairclough 2013; Lang et al. 1993). A considerable experimental bias seems to occur here to the extent that these approaches go against many behaviors performed in front of works of art which exploit an attraction/repulsion relationship, as in the case of the category of the sublime.

The Sublime Enables a Less Problematic Naturalization

Maybe by default, or perhaps because we have the means to do so—in a nutshell, a priori without any objective reason—pleasure and the beautiful have been studied. They are important in aesthetic experience, but all pleasure is not aesthetic. It is important not to confuse the beautiful, aesthetics and art: when it comes to building a neuroaesthetics that aims at becoming a theory of art, one of the main risks is to study the beautiful as if it were a synonymous for art. Only by opening up the cognitive investigations to aesthetic values other than the beautiful can we maintain the crucial interdisciplinary dialog between neuroscientists and both classical and contemporary philosophers of art.

The works of naturalization that focus on the beautiful run the risk of shifting the principle of the field, or even of diluting it in researches that cannot give account for the diversity of aesthetic experiences. It is not possible to study a single pleasure at a hormonal, neuronal or even behavioral level, since the complexity and the integrativity of aesthetic experience makes it possible for the spectator to be satisfied with a work that is, at a physiological level, *unpleasant*. This case is the one which is described by Burke, Kant, Hegel or Schiller in their works on the sublime. The sublime implies unpleasure, fear (or representation of fear), but comes to pleasure. Reductionist naturalist researchers would tell us that it is neither possible to enjoy the sublime, nor the vertigo, nor the imbalance felt at the top of the Tower of Pisa: indeed, their studies would highlight the fact that individuals wince, that beads of sweats form on their foreheads, that they physiologically feel emotions that fall into the category of negative emotions.[2] However, despite all this, some would be satisfied. Let there be no mistake, we do not intend to say that such empirical studies would refute introspection; on the contrary we intend to say that they would lead to propose a theory that would be refuted by the studied system itself, that is to say the set of aesthetic experiences. Thus, trying to naturalize the approbation of the spectator who is confronted with a work of art not only is not a question of aesthetics anymore, but gives also rise to the risk of grafting an over-simplified

---

[2] This criticism can also more generally apply to studies that try to describe aesthetic experience as an ability which would be selected *for itself* by evolution.

determinism onto an experience which involves too many parameters to be modeled by a reductionist approach.

Anjan Chatterjee hypothesized that the lack of interest of research toward the sublime can be explained by the limited data available about the cognitive processes that are involved in the behavior linked with the sublime. He mentioned the metaphor of a person who would search for his dropped coin under the light of a street-lamp because it would be the only place which would be lit, even if he would not have lost it at that place (Chatterjee 2010). Indeed, the sublime is not studied enough in neuroscience, but this metaphor does not seem to bring a satisfactory explanation. In fact, even if the label "the sublime" is poorly used is neuroscience, the experiences linked with the sublime do involve many processes that are widely studied. The processes involved in the aesthetic experience of the sublime, for instance postural imbalance or vertigo, are indeed abundantly studied—because postural imbalance is also associated with many pathological behaviors. There could be an interplay between the study of pathological imbalance in a routine context and the study of the imbalance of a healthy individual in an artistic context: artistic objects indeed imply a considerable particularity in the relationship between individuals and their environment. Imbalance at the levels of posture and of the vestibular system would constitute a relevant observable to naturalize the sublime. What is more, the specificity of the sublime lies in the satisfaction that is taken in an unpleasant situation: fear, which is generally classified as a negative emotion (Ekman 1992), becomes a source of pleasure. Regarding this subject, we can also find an abundant literature about emotions, mainly about negative emotions like fear. It is also quite easy to rationalize fear in light of the theory of evolution: it acts as an alarm to draw the attention of the individual to a danger he or she should avoid. In other words, the aesthetic experiences that can be described as sublime already benefit from real scientific investigations in the field of cognitive science and in the trend of naturalization.

It would be a mistake to believe that neuroaesthetics focuses on the beautiful because the means that are available to study aesthetic experience would not enable to study another aesthetic category. There have besides been some works in cognitive aesthetics dealing with the sublime in general and the situation of imbalance in particular (Noë 2001). These studies have given rise to few experiments, simply because the works of art that were used were large sculptures, which made the practical implementation of the experiments challenging.[3] Yet, many bidimensional works can have an impact on the postural equilibrium of the spectator and could constitute a promising paradigmatic case study. *Contemplation irrationnelle*, a work created in 2003 by Philippe Ramette, is in that sense particularly interesting. In this photograph, we can see a person who is apparently sitting at the edge of a quite impressive precipice. We can quickly realize that this photograph is actually a quite commonplace view that has been rotated one quarter-turn, so that the great

---

[3] We notably think about *Clara-Clara* by Richard Serra, which is an example that Alva Noë took. Since it is a monumental sculpture, any study should only be done in situ.

skyline irremediably becomes an abyss. The road that is winding between small hills becomes a path that is almost vertical. However, the awareness that the landscape has been rotated is not sufficient to suppress the illusion of the precipice because the person that we see seems to be sitting in the correct orientation: his thighs appear horizontal, his back vertical. It would be interesting to study to what extent the perception of this photograph by an individual that would be in front of it, preferentially standing up, stimulates his or her vestibular system and (her) posture. Some studies dealing with the contagion of vertigo suggest that the fact of watching another person who is in a situation of imbalance can lead to a modification of one's own balance. We could thus speculate that imbalance could arise from perceptual processes which, under the influence of visual discordances linked with verticality, do not provide conscience with a steady perception, but with a perception that frequently oscillates between a photograph that would or would not have been rotated. Aesthetic experience thus seems stimulated by various elements, notably the tendency for empathy, vertigo—both caused by real risks or by the illusion of risks—, or the possibility of bistable perception. It could without doubt be possible to list more elements, and it could then be even more difficult to know which one would be specific to the aesthetic experience which is at stake, if we suppose that this question even has a meaning. Therefore, it may be more interesting for aesthetics to study the cognitive processes involved in aesthetic experiences without trying to give account for the particularity of one aesthetic category or another.

Upstream and Downstream Aesthetic Categories

It does not seem possible to naturalize aesthetics, but it is interesting to naturalize the routine cognitive processes that are involved, in a non-routine manner, in aesthetic experiences. If only for the comparison between the beautiful and the sublime, we realize that studying the specificity of one will not enable to understand that of the other: the beautiful and the sublime are very different as far as the cognitive processes and the link with the theory of evolution we could draw are respectively concerned. Indeed, the beautiful is often considered as a derivation of an acquired behavior, but it is harder to explain the pleasure that the individual takes in a context that stimulates a state of alarm from a physiological point of view. As we have highlighted from the introduction of this chapter, aesthetic experiences involve numerous cognitive processes. Since it does appear that one of them is not more particular than another, we could hypothesize that aesthetic experience emerges from a common way of using cognitive processes. Regarding this hypothesis, we can detect a constant in the philosophical history of aesthetics: aesthetic experience is induced by a sensitive awareness of our own cognitive processes even though our attention focus on the outside world. This statement is a contemporary and generalized rephrasing of the idea that the awareness through the sensitivity of the free play of faculties is a reflective judgment that Kant supposed to be at the basis of the beautiful (Kant 1790).[4] This hypothesis is in keeping with the integrative idea that aesthetic experience involves a split attention (focused on oneself and on the world), or involves a self-reference to one's own mental processes (Vessel et al. 2012, 2013). We adopt such a characterization of aesthetic experience as a general working hypothesis because it gives account for the possibility that aesthetic experience can involve numerous cognitive processes: aesthetic experience is a sensation induced by the way cognitive processes, whatever they may be, adapt as successfully as they can to non-routine and highly cultural situations. Thus, the most convincing way of trying to naturalize upstream aesthetic categories like the beautiful and the sublime is to find the observables that indicate the adaptability of cognitive processes, i.e. the reconfiguration of perception. Naturalizing reflective judgment would be a better way to *observe* aesthetic experience. Nevertheless, the question of knowing whether this knowledge will help the aesthetician to give a better account of artistic experiences remains open: naturalizing reflective judgment is a response to a speculative will of understanding aesthetics in its most abstract issue (Trentini 2014). On the contrary, in order to build an aesthetics that is able to give account of artistic experience downstream aesthetic categories, it would be more interesting to understand the steps leading to reflective judgment rather than reflective judgment itself. To translate the words of the introduction of *Naturaliser l'esthétique* written by Jacques Morizot: "the challenge we have to take up is to understand how routine mechanisms are able to generate a non-routine vision" (Morizot 2014).[5] It could be tempting to hypothesize that the understanding of these routine mechanisms would not bring anything new to the understanding of aesthetics, but aesthetic experience can only emerge from breaking out routine. Because the experience is non-routine, cognitive processes must adapt to a new configuration; because they must adapt in a non-routine way, a particular feeling emerges from their adaptation. In that sense, a complete rupture with the evolutionist theories is not desirable: we have to understand how cognitive processes have adapted to the environment at the scale of evolution and how they can adapt at the scale of the individual—by being flexible or plastic—, but we should not globally consider aesthetic experience as a selected or a counter-selected ability. We should consider aesthetic experience as involving abilities that are acquired both through culture and by evolution.

---

[4] Semir Zeki seized the concept of the free play of the faculties to make it the cornerstone of his naturalization at the neural level; it seems to us that his modularist approach—as defined by Fodor—cannot enable to understand aesthetic experience. In fact, the cognitive fluence that he studied is specific to the beauty. We thus loose the specificity of reflective judgment to only keep fluence. Not only this study cannot enable to establish a philosophy of art, but it also fails to pave the way for a generalization of the beauty on the other aesthetic experiences.

[5] "Le défi à relever est de comprendre comment des mécanismes de routine sont en mesure d'engendrer une vision qui ne l'est pas".

Conclusion

If we were to put forward a particular skill of the aesthetician—and probably of the art critic as well—we could mention the ability of making a singular experience communicable, and as a consequence the ability of conducting a good introspection, that is to say the ability of correctly grasping what is going on in their bodies, at the level of their organs, of their senses, and the ability of linking as accurately as possible these sensations to the multiple thoughts that went through their minds. This undertaking is of course not infallible, and we can suppose that the more relevant the introspection, the easier the communicability. Since we are dealing with introspection, I allow myself to speak in my name, about a personal aesthetic experience.

I discovered the works by Marcius Galan at the *White Cube*, gallery in London, in the summer of 2013, and I once again saw one of these works in the exhibition *Inside* at the *Palais de Tokyo* in Paris in the winter of 2014. Despite my research between these two moments, for instance about the way in which perception can generate the illusion of a surface where there is none, about the interpretation of the variation of colors that the presence of a glass plate would have caused, I felt an intense experience on both occasions. In other words, even if I was aware of the cognitive processes that were involved to create the illusion, the illusion still persisted. Thus, I do not think that the naturalization of aesthetics can weaken aesthetic experience—nor can it dictate aesthetic experience, since the understanding of the processes do not necessarily make a work pleasant to someone who did not like it in the first place. However, by putting forward the coupling between perception and action, I can make the wish of going through the intangible surface communicable and this is precisely what I did at the *Palais de Tokyo*: I waited for people to enter the room and I threw myself into the virtual window. Against all odds, I did not feel at ease. It may seem ridiculous, but my body was put into a state of alert: I was presumably *afraid* of hitting the glass plate. My cognitive processes apparently reacted as if the glass plate had been true. I thought that this moment was particularly interesting, and particularly promising as regards the theory of embodied aesthetics.

Sometimes, in front of a work of art, I have the intuition that one thing or another has occurred in me and that my perception has adapted in one way or another, for one reason or another. If convincing experiments that clearly refute my hypothesis have been carried out, I do not want to trust my introspection to use it to comment on the work. If on the contrary experiments of naturalization go in the same direction as my introspection, I feel comforted in my view. In other words, naturalization of cognitive processes, even apart from aesthetic experience, represent clear benchmarks in my research, which help to hold back a misleading introspection or to clarify a relevant but too confused introspection. Thus, knowing that experiments have shown that most people feel unbalanced while watching a funambulist nourishes my research on Philippe Ramette. Knowing that experiments dealing with disown (Guterstam and Ehrsson 2012)—which is the feeling of not belonging to one's own body—were put forward nourishes my research on the works by Ann Veronica Jannsens. The list could go on and on, yet, further research would still be required in order to obtain relevant data to carry out a work of embodied aesthetics dealing for example with conceptual art. I am nevertheless perfectly prone to believe that such data can be obtained.

These few elements having been established, aesthetics seems to have a lot to gain from physiological studies dealing, on the one hand, with the capacity of cognitive processes to adapt and, on the other hand, with the capacity of these adaptations to be felt by individuals. It is to our mind at these two levels that naturalization can prove to be beneficial to aesthetics.

References

Cela-Conde C et al (2004) Activation of the prefrontal cortex in the human visual aesthetic perception. Proc Nat Acad Sci U S A 101:6321–6325

Cela-Conde C et al (2013) Dynamics of brain networks in the aesthetic appreciation. PNAS 108 (supp 2):10454–10461

Chatterjee A (2010) Neuroaesthetics: a coming of age story. J Cogn Neurosci 23–1:53–62

de Tommaso M et al (2008) Influence of aesthetic perception on visual event-related potentials. Conscious Cogn 17:933–945

Dutton D (2009) The art instinct. Steven Pinker, New York

Ekman P (1992) An argument for basic emotions. Cogn Emot 6:169–200

Grammer K et al (2003) Darwinian aesthetics: sexual selection and the biology of beauty. Biol Rev 78(3):385–407

Guterstam A, Ehrsson HH (2012) Disowning one's seen real body during an out-of-body illusion. Conscious Cogn. doi:10.1016/j.concog.2012.01.018

Ishizu T, Zeki S (2011) Toward a brain-based theory of beauty. PLoS ONE 6:e21852. doi:10.1371/journal.pone.0021852

Kant I (1790) Critique of the Power of Judgment. University Press, Cambridge, 2000

Kreplin U, Fairclough SH (2013) Activation of the rostromedial prefrontal cortex during the experience of positive emotion in the context of esthetic experience. An fNIRS study. Front Human Neurosci 7(art.879)

Lang PJ et al (1993) Looking at pictures: affective, facial, visceral and behavioral reactions. Psychophysiology 30:261–273

Morizot J (ed) (2014) Naturaliser l'esthétique? Questions et enjeux d'un programme philosophique. PUR, Rennes

Munar E et al (2012) Lateral orbitofrontal cortex involvement in initial negative aesthetic impression formation. PLoS ONE 7(6):e38152. doi:10.1371/journal.pone.0038152

Nietzsche F (1889) Twilight of the Idols. Oxford world's classics, 2008

Noë A (2001) Experience and experiment in art. J Conscious Stud 7(8–9)

Smith CUM (2005) Evolutionary neurobiology and aesthetics. Perspect Biol Med 48(1):17–30

Trentini B (2014) Peut-on faire une esthétique incarnée du jugement réfléchissant? In: Morizot J (ed) Naturaliser l'esthétique? Questions et enjeux d'un programme philosophique. PUR, Rennes

Vartanian O, Goel V (2004) Neuroanatomical correlates of aesthetic preference for paintings. NeuroReport 15:893–897

Vessel E et al (2012) The brain on art: intense aesthetic experience activates the default mode network. Front Human Neurosci 6(art.66)

Vessel E et al (2013) Art reaches within: aesthetic experience, the self and the default mode network. Front Human Neurosci 7(art.258)

Zeki S (1999) Art and the brain. J Conscious Stud 6(6–7):76–96