Title:

The neural selection and the emergence of 'beauty canons' as signaling codes in co-evolving species

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Abstract

Widespread opinion wants beauty to be pleasant and aimless, this assumption biased Darwin's explanation of sexual selection. Conversely, Wallace hypothesized that showy and symmetric sexual traits correlate with vigor and health and he placed ‘aesthetic’ preferences within the natural selection. The controversy has continued until today.

To understand the role of beauty canons in communication, the focus was on the flower-pollinator cooperative system as a model, were flower evolution embodies the natural history of pollinators' preferences.

Optimum for a signal requires energy efficiency, high signal-to-noise ratio, and intelligibility. It involves pollinator perception mechanisms that, in turn, induce co-evolutionary feedback on signal traits. In fact, the flowers physical and hedonic properties correlate with the basic perceptual, motivational, emotional, and learning mechanisms of pollinators.

It is proposed that pollinator behavior, unmasking a preference, reveals the ability to evaluate an expected benefit. Features such as a relative simplicity, redundancy, and regularity of stimuli facilitate perception and memorization and are essential elements for communication between co-evolving species. They improve signaling to satisfy the need for easy and fast recognition. With these properties, a stimulus is adaptive and rewarding per se and may be an ideal conditioned stimulus in associative learning.

Among the most conspicuous signals, pollinators learn to recognize and choose those associated with nectar, thus favoring the evolution of flowers that are not only ‘beautiful’ but also ‘honest’ in reporting a reward. Beauty is an emergent property, and studying communication and perception we may understand the origin of some beauty canons.

Keywords: pleasure, perceptual fluency, aposematic signal, repetition in learning, sensory bias

Contents

Introduction

- The problem of preference

The subjective preferences guide mate choice or individual selection among cooperating species. The selective pressure thus exerted has profound evolutionary consequences but the mechanisms of choice are not clear and often explained as purely aesthetic. Ancient and medieval philosophers thought that beauty was an intrinsic characteristic of the admired object and described it as particular mathematical relationships or symmetries. Charles Darwin, however, argued that the sense of beauty depends on the nature of our mind. He argued that the aesthetic basis of the various traits of individuals derives from selective mechanisms, especially sexual ones. Darwin, in his “Notebook M”, stated that beauty is an instinctive feeling while in “The Descent of Man” he recognized that “the eye prefers symmetry or figures with some recurrent elements” (Darwin 1871). People consider beauty pleasant but, erroneously, they considered beauty pleasant for itself, without any reason (Feagin 1999). This assumption biased Darwin's explanation about the evolution of particularly showy secondary sexual traits, such as the peacock tail, for which he assumed that the choice of females depends on their arbitrary aesthetic preference without any particular adaptive purpose. On the other hand, Alfred R. Wallace suggested the idea that conspicuous sexual traits were an honest sign of individual health and vigor. With this assumption, he suggested that mating preferences could comply with the logic of natural selection without other explanation, as Prum pointed out (Prum 2012). However, the reason why the brain prefers ‘beauty’, or why attractive signals should also be honest, remain unanswered questions.

Among the revolutionary ideas presented by Darwin is that of coevolution. From the literature we know that coevolution of predator-prey species induces adaptations in both, making the predators more capable to catch prey and the prey more skillful in escaping. What happens when evolution is cooperative and living beings need to recognize each other? Along with the widely studied example of sexual selection (Prum 2013), other cases of emerging beauty occur among different species visited by pollinators and seed dispersers e.g. in flowering plants, in social mimicry (Moynihan 1968) and in warning signals (Roper 1987). In all these cases, the effects of natural selection seem overridden by an ‘*aesthetic selection’* (Darwin 1871; Enquist and Arak 1998; Prum 2012).

- About the use of the word ‘beauty’

The word 'beauty' here is intended in common sense, it indicates the property of the stimulus of evoking pleasure in a human observer, i.e. an inner signal of good adaptation, a positive emotion, regardless of other stimulus meanings. This is supposed to apply to humans and it is assumed that to some extent it may also apply to other animals. Starting from some empirical observations it is possible to correlate the evoked pleasure to structural and physical features of a stimulus. Some are relatively simple as brightness, color, and contrast, or perfume, others are more structured as symmetry, regularity, and harmony (Enquist and Arak 1994; Feagin 1999; Fechner 1876). The variety of associated features suggests that beauty is not a single parameter. Its evaluation is possible indirectly through the behavior induced in the observer in terms of attraction and preference. This makes it possible to study beauty reactions even in non-human subjects. The beautiful stimuli capture the attention, are fluently perceived and recognized, rapidly learnt, memorable, and rewarding (Guilford and Dawkins 1991; Reber et al. 2004). The signals presenting these properties are ideal conditioned stimuli in associative learning (Guilford and Dawkins 1991).

- The hypothesis of beauty canons as natural codes of communication

This study aims to discuss a new function of signal beauty considering some facts accepted in different disciplines and dispelling some commonplaces such as the arbitrariness of preference for beauty. Conversely, I explore the possibility that beauty is a phenomenon emerging from a process of cooperative evolution with the function of enhancing communication between organisms. I hypothesize that beautiful traits correlate to physical and structural characteristics of sensory stimuli that speed up perception in a specific observer who, in turn, can achieve a better adaptation. This explains why beautiful stimuli are pleasant and preferred in place of random sensory patterns. Beautiful stimuli are not necessarily important per se but when they are contingent on significant events, following the paradigm of classical conditioning the observer learns to use the former as predictive clues of the latter. The physical and hedonic properties of flowers are discussed, comparing them with the basic perceptual, motivational, emotional and learning mechanisms of the observer. Only by understanding the implications of these neural mechanisms is it possible to pass from the mere observation of the emerging beauty to a causal explanation of the process. Moreover, considering that many animal species including humans present these basic functions of the nervous system, it is possible to explain the general appreciation for some beauty canons.

The beauty of flowers as an emergent quality

The focus is on the beauty of biotic pollinated flowers since the flower-pollinator system is one of the simplest models of emerging beauty that allow a cause-effect analysis of the phenomenon. It is assumed that the need for signaling and localization, implicit in the cooperative relationship, is a cause of the evolution of flower characteristics. It is therefore considered the pre-existence of pollinators with respect to flowers. This suggests that pollinators are responsible for the appearance of flowers in their current form. In this role, their perceptive and nervous system with the ability to learn and guide their movements and preferences would have played a fundamental role.

- The innovation of flowering plants

Flowering plants are present in a wide variety of forms and are the greatest advance of plants adapted to life on land. Their innovation, the flower, is the product of plant-pollinator coevolution (Schiestl and Johnson 2013). It represents the reproductive part of angiosperm plants. In the flower, stamens and carpels are highly specialized for reproduction, and petals and other parts are devoted to the protection and the special function of attracting pollinator animals that pass from flower to flower transferring the pollen grains with relatively high specificity and no waste (Proctor et al. 2012). Only flowers detected by pollinators can receive their visit and gain a higher possibility of reproduction. Within the limits of their sensory and cognitive abilities, pollinators analyze the environment in their search for flowers. Similarly, the characteristics of the flower closely correspond to the recognition capacity of the pollinating animals

- Flowers from genetic variability and pollinator selection

From fossil specimens, we know that the first fossils of flowering plants appear in the early Cretaceous (Friis et al. 2010; Frohlich and Chase 2007; Magallon et al. 2015). By the end of the Cretaceous, angiosperms dominated the flora. Great insect diversification preceded that of flowering plants by more than 100 million years. Based on the anatomy of their feeding apparatus, all major insect types existed before angiosperms (Cai et al. 2018; Labandeira and Sepkoski 1993; van Eldijk et al. 2018) and four gymnosperm pollinator modes were present during the mid-Cretaceous angiosperm radiation (Peris et al. 2017). It is reasonable to assume that pollen-feeding animals have most frequently visited the plants that most stimulated their sensory systems, attracting their attention and initiating a directional selection (Rieseberg et al. 2002). This suggests that angiosperms refined their floral attributes to comply with the selective pressure of pollinators that, in turn, spent less time foraging. The initial preference led to positive feedback, causing a continuous refinement of the preferred traits (Boughman 2002; Schiestl and Johnson 2013).

Animals and plants influenced each other generating some constraints and the driving force for their further coevolution (Pauw et al. 2009; Zhang and Wang 2017). However, it is necessary taking into account that flowering plants and pollinators affect each other with different mechanisms. While the plants evolve with a mechanism of variable reproduction and selection, the animals have an extra gear. They can direct the evolutionary process by adapting their behavior much more quickly by means of the learning abilities of the nervous system (Lynn et al. 2005). Since pollen-feeding insects were present before flowering plants, we can assume that they oriented themselves during foraging, looking at conspicuous perceptive stimuli associated with the richest sources of food to maximize their harvest. Pollinators and flowers have tuned in to each other by choosing code symbols from the traits generated by the natural variability of the plants. Symmetric forms, colors, and fragrances are these symbols. Pollinators followed their preferences, depending necessarily on the physiological properties of their sensory organs. Moreover, their neural networks determined the capacity to find the invariant features of sensory patterns, and the associative learning established the possibility to maximize the reward.

The selective nervous system

The flower as a sensory stimulus has objective physical properties, its appearance, but a subjective meaning dependent on the motivations of the observer. It is assumed that the meaning is the effect that the stimulus causes in the observer both involuntary, as in reflexes and emotions and voluntary behavior. Pollinators show different attention to the phenotypic characters of the flowers; therefore, flowers undergo a different selective pressure that will promote the most attractive ones. Interestingly, these traits are based on aesthetic canons.

- The dual nature of sensory stimuli: structural information and significance

Flowers are physiological stimuli for pollinator animals. In sensory physiology, a stimulus is a detectable change in the external or internal environment of a living being. It is a physical or chemical form of interaction with the receptors. The interaction triggers sensory transduction, providing nerve signals for perception and adaptive actions. A sensory stimulus has a dual quality: 1) its physical nature, as in Pavlov's experiment, where we can *objectively* describe the ring of the bell, its frequency, intensity, and duration (Schacter and Wagner 2012). These physical parameters represent the intrinsic structural information of the stimulus and are independent of the observer and 2) its significance, which concerns the effects on the receiver i.e. sensory transduction, analysis, and response. Whereas structural information is a stimulus component independent from the actual observer, the perception and evaluation of the stimulus is extrinsic to the stimulus and depends on the actual observer (Garner 1974; Guilford and Dawkins 1991). In Pavlovian conditioning, bell sound may be meaningful for the dog predicting the food arrival or not, depending on dog ability: 1) to sense the sound, and 2) to learn from experience recognizing the relationship between the bell sound and food. After a learning process, stimuli previously neutral become significant (conditioned) and predictive of hedonic experience.

- Choice of the floral traits and improvement of communication parameters

Although the physical appearance and meaning for the pollinator have evolved together in the flowers, for clarity I will begin to consider the first separately from the second.

Manipulation of hue, saturation, and value of color in studies on designing print ads, showed that a higher level of value and saturation of colors lead to a greater appreciation of the advertisement (Gorn et al. 1997). Naturalists have long accepted that angiosperms evolved colorful and scented flowers as advertisements to insects and other pollinators (Darwin 1862; Müller 1873; Spregnel 1793). If we assume that the floral traits meet the canons of classic beauty, what is their functional role in floral-pollinator evolution?

Interactions in coevolving species present a two-sided problem: the sensory capabilities of the seeker and the characteristics of the targeted species (Pauw et al. 2009). If the target is a prey, it will benefit from the sensory limits of its predators and will possibly undergo a selective pressure which will favor traits of camouflage and invisibility (Stevens 2007). Conversely, if the target has an advantage from appearing to other living beings, as in a plant that benefits from pollination, selective pressure will favor visible and attractive plants (Schiestl and Johnson 2013). The sensory possibilities of the recipient, often referred to as sensory bias, determine which features of the stimulus can be detected. In addition to the limited receptors bandwidth, detection depends on the limited possibilities of nerve networks to process sensory patterns. More simple and repeated configurations with symmetric elements are preferred and easily memorized. The constituent characteristics of animal fine perception are responsible for the sensory biases suggested to explain exaggerated characters following sexual selection, but also for some general properties of pattern detection common to animals (Benard et al. 2006; Chittka and Raine 2006; Giurfa et al. 1996; Gumbert 2000; Horridge 2009; Kelber 2002; Lynn et al. 2005) and even to artificial neural networks (Enquist and Arak 1994; Johnstone 1994; Roper et al. 2017).

- Sensory detection in pollinators

Karl Von Frisch demonstrated that bees easily distinguish a range of colors (Backhaus 1993). Since he published his work, rigorous implementation of psychophysical and neurobiological methods has produced a huge amount of data (Avargues-Weber and Giurfa 2014; Dyer et al. 2011; Renoult et al. 2014). See van der Kooi et al. (2018) for a recent review on plant-pollinator visual signalings such as chromatic and achromatic contrast, hue, saturation, brightness, and less common types of visual signals, including gloss, fluorescence, polarization, and iridescence. Since relevant stimuli must match sensory receptor characteristics, the pollinator photoreceptors sensitivity is in tune with the colors of the preferred flower species (Papiorek et al. 2016; Vasas et al. 2017), as well as the chemical sense selectivity is adapted to the floral scents (Auffarth 2013;

Chittka and Raine 2006; Proctor et al. 2012). Indeed, the visual apparatus of insects has elementary functions similar to the simplest retinal functions. Pollinators have different types of photoreceptors with opponent visual receptive fields that differ in spectral sensitivities (Hempel de Ibarra et al. 2014; Horridge 2015; Stach et al. 2004) and display a preference for green and color contrast (Gaskett et al. 2017; Osorio and Vorobyev 2005; Renoult et al. 2013). They can select quantitative variation in floral coloration, possibly determining its evolution (Lynn et al. 2005). If the flower color is different from the background giving a higher signal to noise ratio, it facilitates the pollinators search activity (Naug and Arathi 2007; Renoult et al. 2013). Recent studies show that pollinators can also benefit from multisensory integration by improving their fluidity of recognition if flowers have multiple detectable floral traits. (Glover 2011; Kinoshita et al. 2017; Leonard and Masek 2014; Telles et al. 2017).

The limited perceptive possibilities of a sensory apparatus point to conspicuous stimuli. If insects preceded flowering plants evolution by more than 100 million years, they were most probably the protagonists of the first selection of colors based on their photoreceptor capabilities. Further confirmation of the driving role of pollinators on flower evolution comes from studies showing that even many typical floral scents evolved earlier than flowers, as they were first present in insects themselves (Schiestl 2010; Schiestl and Dotterl 2012). Thus, the aromatics that exerted an attraction within a species seem to have appeared in angiosperms as a result of the selection made by the pollinators themselves, accustomed to those scents. It should be reductive, however, thinking that the sensory receptors alone give the pollinators prominence in the coevolution with flowers. As discussed below, their cognitive abilities are another powerful means that allow potential pollinators to prevail on plants being the main driving force in pollinator-flower coevolution (ten Cate and Rowe 2007).

The pollinators contribution in defining the characteristics of the visited flowers becomes evident if we consider those pollinated by the wind. The latter are not showy and fragrant and produce less nectar. In addition, to perform their function they have to produce and spread an enormous quantity of pollen (Shukla 1998).

- Recognition of simple patterns, symmetry, and regularity

Among the many, perhaps infinite, characteristics of an object, the observer easily captures simple features as symmetry, regularity, etc. when present.

Simplicity is the attribute of a sensory stimulus that shows the minimum complexity or structural information, allowing a robust recognition in its environment, given a determined perceptive apparatus (Li and Vitányi 2008). If little information is analyzed, the cognitive task is easier, so simplicity is preferable to complexity. E.g., the sign-stimuli or releasers, animal signals that trigger instinctive behavioral sequences (fixed action patterns) in the receiver; ethologists observed that these very effective and specific signals tend to evolve toward simplicity, in other words, minimal structural information and high subjective significance (Russell 1943; Ryan et al. 2001; Tinbergen 1951).

A similar consideration can be made for the other conspicuous and alluring features, namely the canons of beauty (Kayaert and Wagemans 2009). Gestalt scholars postulated that symmetry is one of the grouping principles of our visual perception and presents a high level of “goodness”, i.e. salience or perceptual strength (Garner 1970; Koffka 1935; Köhler 1929). The object regularity and symmetry facilitate fine perception increasing the ease of classification of object's new views and diminishing the effect of the point of view on the classification efficiency. I.e., looking at the symmetrical object from different angles will need fewer views than asymmetrical objects to reach the same level of general knowledge (Liu and Kersten 2003; Liu et al. 1995; Rock and DiVita 1987; Vetter et al. 1994).

Detection of vertical symmetry is easier (Palmer and Hemenway 1978), but versatile neural mechanisms can also detect symmetry on oblique axes (Barlow and Reeves 1979). Empirically, a regularity presents a higher salience, and its detection is easier even with noise (van der Helm and Leeuwenberg 1996). Symmetry perception seems to work as a filter in pattern recognition, which identifies symmetric patterns of stimuli and classifies symmetric shapes preferentially as foreground objects and irregular shapes as background (Bahnsen 1928; Driver et al. 1992; Machilsen et al. 2009).

Living beings incorporate various forms of symmetries that make them conspicuous and detectable (Attneave 1955; Barlow and Reeves 1979; Enquist and Arak 1994; Enquist and Johnstone 1997; Jansson et al. 2002; Swaddle 1999; Tyler 2002). Noteworthy, insects prefer symmetrical flowers (Moller and Sorci 1998). Botanists have been studying flower symmetry variants for more than a century (Delpino 1887) and the analysis of flowering plant lineages has shown that bilateral flower symmetry evolved from radial symmetrical ancestors (Cubas 2004; Endress 2012; Endress and Doyle 2009; Hileman 2014).

Interestingly, symmetry occurs in many forms of biological communication where it presents important advantages in transmission and detection. Important to note that easy identification relies both on the perceptive system and the object observed.

In the first stage of vision, the visual apparatus detects light, contrast, and colors, the basic elements of beauty canons and the necessary components of any other feature (Meister and Tessier-Lavigne 2012). Subsequent elaboration of visual information allows more features recognition, as symmetries, identified early in perception (Bertamini and Makin 2014; Finke et al. 2017; Kayaert and Wagemans 2009; Koning and Wagemans 2009; Makin et al. 2015; Treder 2010; van der Helm and Leeuwenberg 1996; Wagemans 1995; Wagemans et al. 1991; Willis and Todorov 2006). A mirror symmetry, for instance, is readily detected in humans and animals (Mach 1914; Wagemans 1995) and recognition of symmetry in textured patterns can take place in as little as 50 ms (Julesz 1971). Non-familiar randomly generated symmetric images detection suggests the poor role for memory in the task (Julesz 1966). Interestingly, the preferences for bilateral symmetry in flower-naive bumblebees is innate (Rodriguez et al. 2004). The impressively rapid brain reaction to 'beautiful' stimuli confirms that the perceptive systems qualify as beautiful the physical characteristics of the stimulus that does not need complex analysis and present robust recognition with perturbations, based on low structural information, redundancy, and invariance from different viewpoints.

Symmetrical patterns have repeated elements depending on the specific configuration. An animal on seeing domain regularities (in time, space, etc.), will probably be able to predict what happens next in that domain as by a few predictive details could infer the entire image. Note that regularly repeated features are also a necessary condition for the learning experience (Holland and Schiffino 2016).

- Repetitions in beautiful patterns and learning

In the human evaluation of beauty, one characteristic is some variability of its value. The physiological response to a beautiful stimulus can change depending on the subject and from time to time in the same subject. E.g., experiments show that repeated exposure to a certain stimulus increases its positive evaluation because of increased fluency of perception (Inoue et al. 2018; Leynes and Addante 2016; Reber et al. 2004; Zajonk 1968). These observations are consistent with the learning capabilities of nervous systems that can change the hedonic value of a stimulus (Berridge and Robinson 2003).

Neural synaptic plasticity implements learning processes, well described in animals even at a low phylogenetic level. (Dawson et al. 2013; Glanzman 2005) While genetic heritage directs interactions with the environment in predetermined ways throughout the individual life, learning from experience allows to generate new adaptive behaviors in a short time, and change them several times during life span. Priming, associative and non-associative learning are among the simplest ways the brain interacts adaptively and are very interesting as far as beauty perception is concerned. Stimulus repetition is fundamental for learning as recurring events can become predictable (Schacter and Wagner 2012). With associative mechanisms, it is possible to learn and memorize the existing relation between events or stimuli (Pavlovian conditioning) or between a behavior and its consequences (operant conditioning). The subjective evaluation of the results achieved during the learning process is, in general terms, pleasure or displeasure. These learning paradigms share a common characteristic: they induce an adaptive reaction when the circumstances occur again.

Most learning studies adopted protocols where the repetition of experimental tests was in the time domain. I.e., detecting some coincidence or regularities over time, the experimental subject learns to anticipate future actions and to increase the likelihood of success. However, repeated patterns in the spatial domain may be suggestive of spatial inferences as well. Our brain, for instance, completes an image despite the physiologic blind spot present in the visual field, caused by optic disc; the brain seems to make predictions analyzing the stimulus attributes in the scotoma surround. Experimental evidence suggests a perceptual filling in (Komatsu et al. 2000; Ramachandran and Gregory 1991). Beautiful patterns for their characteristics of harmony and redundancy are susceptible to prediction and generalization and are easily perceived and memorized.

Beautiful stimuli: emotional and associative processes

Beautiful stimuli induce a pleasant emotion. This behavioral reaction of the observer is measured experimentally in pollinators as an attraction or a preference. It is assumed that pleasure is induced by the better adaptation resulting from easy perceptive recognition. Conspicuous stimuli are excellent conditioned stimuli. Among these, pollinators learn to visit more frequently those that offer greater rewards, i.e. significant to the biological needs of the animal. Therefore, pollinators exert an evolutionary pressure towards both beautiful and generous flowers.

- The experience of beauty as an emotional process

Beauty induces a pleasurable emotion in humans (Barrett and Bar 2009; Pecchinenda et al. 2014; Winkielman and Cacioppo 2001). Therefore, any theory of beauty must combine perceptive and emotional processes. Although the definition of emotion refers to humans, it involves adaptive behaviors that apply across phylogeny (Anderson and Adolphs 2014; Darwin 1872; Mendl and Paul 2016). In humans, the term emotion refers to both physiological responses e.g. changes in heart rate, ventilation, sweating, some somatic behaviors, etc., and the accompanying conscious experience of feeling, i.e. the perception of one's own state and the situation that generated it (LeDoux J.E. and Damasio 2012). Darwin claimed that even insects express emotions (Darwin 1872). While animals cannot tell us if they have a feeling, they certainly present measurable physiological responses and recent research confirms that invertebrate and insects may have emotion-like states (Anderson and Adolphs 2014; Bateson et al. 2011; Fossat et al. 2014; Gibson et al. 2015; Mendl and Paul 2016; Niedenthal et al. 2009; Perry et al. 2016). Pleasure or displeasure are emotional components that depend on stimuli and on their outcome, but also on the perceiving subject internal state or motivation. I.e., if a warm stimulus evokes pleasure in a hypothermic subject, the same stimulus may annoy the subject when it is overheated. These emotional reactions correlate to expected benefits or dangers of stimuli on the organism homeostasis and are characteristics of adaptive behavior. (Berridge and Kringelbach 2015; Cabanac 1979; Cabanac 2002; Frijda 2010; LeDoux 2012). Although animals cannot verbally report their feelings, their behavior can reveal an attraction to stimuli based on the canons of beauty (Guilford and Dawkins 1991). The beauty of the stimulus structure causes an affective response, i.e. the emotional reaction induced in the receiver given that "affect" means to produce a change, as described by Barrett and Bar (2009). To understand the pleasure and gratification induced by beauty is necessary to clarify the meaning of sensory information considering the motivations of the observer. The stimulus features detected by a living being have somewhat significance for them. The brain must recognize the sensory patterns as relevant or not as soon as possible, to trigger the proper motor response to maintain life and homeostasis. These needs represent the driving force that oriented sensory evolution, the mechanisms of sensory pattern analyses and a useful and consistent internal representation of the world. Nervous circuits are selected along a phylogenetic tree and during individual development, where experience plays an important role, and continuous learning refine them (Sanes et al. 2012). We should not think of a perceptive system as being open to any input, rather, of a limited system which focuses on signals subjectively salient.

Keeping into account that the subjective experience of beauty is an early elicited emotion accompanied in humans by a feeling of pleasure (Brielmann and Pelli 2017), we must assume that it satisfies the need for easy and fast recognition of the stimulus pattern and is, therefore, adaptive and rewarding per se. Note that this hedonic value is distinct from that of the stimulus meaning (see below).

Patterns invariant in time and space are directly recognized and useful in associative learning, easily memorized and predicted. Symmetric patterns with low structural information easily induce the feeling of beauty and spontaneously cause positive affect (Pecchinenda et al. 2014), while patterns presenting irregularities or oddities likely induce an error signal, i.e. the difference between received and expected stimuli. The affective valence of error signals is supposedly negative, because an organism tends to assume the worst, as the cost of a missed alarm is potentially larger than the cost of a false alarm (Van de Cruys and Wagemans 2011). Symmetric objects are clearly distinguishable from the background and are fluently detected. They are part of the canons of beauty; these canons allow the so-called *processing fluency* measured in psychology, i.e. easy recognition of the stimulus identity (Palmer et al. 2013; Reber et al. 2004).

Although some basic mechanisms of learning seem fundamental for beauty perception, elementary forms of beauty do not seem to need specific learning to be appreciated, e.g. starlight or sunset colors. This suggests that the pleasure of beauty is a continuum from simple sensory stimuli, fluently detected by hard-wired nerve structures, to less simple ones that need nerve plasticity and learning ability. In all cases, pleasure would come from satisfying the vital motivation to perceive and comprehend the environment. The pleasure of beauty could begin with the supposedly modest pleasure of perception, but the latter should not be underestimated. Indeed, it seems the simple pleasure of breathing; only when there is no air one does realize how great it is.

Since a prompt and precise interpretation of sensory stimuli is vital for survival and adaptation, it is not surprising that *all* living beings, including humans, find easily recognizable sensory patterns more rewarding than others equally significant but barely detectable. Although there may be many neural strategies that observers can adopt for the identification of a particular object, as a result, the processing fluency may present some differences from subject to subject, for the same stimulus (Reber et al. 2004).

- Meaning is independent of the form

Example of a meaningful stimulus is the Pavlovian unconditioned stimulus; anyone that induces an adaptive response, such as the food for which dog produces saliva or a painful stimulus that induces withdrawal behavior. However, stimuli, not significant-per-se can be noticeable, provided they are physically detectable and have previously been associated with meaningful events, as they become predictor signals, conditioned (Holland and Schiffino 2016; Kandel and Siegelbaum 2012; McGann 2015).

An interesting example is aposematism, the case of those living beings that exhibit conspicuous warning signs with bright colors and symmetrical patterns that we can define at first sight as beautiful and pleasant, but that represent signals with a repulsive meaning for potential predators because they are indicative of poisonous or dangerous organisms (Cuthill et al. 2017; Gamberale-Stille et al. 2018; Ruxton et al. 2004). In this case, unlike flowers and pollinators, both species benefit from avoiding each other. The potential preys, with clear warning signals, become more evident to predators who have learned to associate signals otherwise beautiful and pleasant, with unpalatability and to avoid them. It is interesting to note, however, that the same signals are attractive for mating (Rojas et al. 2018).

On the other hand, flowering plants can be very visible to herbivores. This led the plants to develop very effective chemical and physical adaptations to reduce the impact of herbivores. In this case, for the considerations made above it is possible to speculate that the characteristics of certain flowers that attract pollinators may instead be warning signals indicating the presence of toxins for some herbivores. Well documented is the case of flowers that produce odorous signals that induce attraction in pollinators while they repel antagonistic visitors (Junker and Blüthgen 2010).

- Beauty and honesty: beautiful patterns as conditioned stimuli

From a neuroscientific perspective, symmetries may arise during evolution because of the selective functioning of recognition systems (Enquist and Arak 1994; Enquist and

Johnstone 1997; Jansson et al. 2002; Johnstone 1994). Of course, this would not exclude other possible functions of symmetry, e.g. motor symmetry (Hollo 2017). The need for prompt identification of a target in a context of cooperation has involved that the observer, based on original perceptive possibilities, has focused on some initial traits and influenced their subsequent evolution (Lande 1981). We must consider that the optimum for the structural information component of a signal requires, among other things, energy efficiency, high signal-to-noise ratio, and signal intelligibility. The first condition is in balance with the others (Endler 1993; Endler and Basolo 1998). Optimal equilibrium can change from case to case as in Fisherian runaway where an innate perceptive bias of the female is supposed to influence sexual selection favoring males with exaggerated and expensive hereditary traits, for example, the large tail of the peacock (Fisher 1930). Among other explanations, I would suggest that a decreased cost of perception for the receiver might compensate the cost of a very conspicuous signal, as communication burden involves both parties in a co-operative system, and the evolution of a powerful perceptive system is possibly more demanding than the evolution of a big tail.

In classical antiquity, beauty was an indicator of positive characteristics such as good qualities and virtues. Mating preferences for symmetry have been correlated to honest information about mate quality (Grammer et al. 2003; Zahavi 1975). It seems reasonable to assume that asymmetric appearance in an otherwise symmetric species is a signal of the phenotypic or genotypic bad quality of the bearer. However, asymmetry is not necessarily the result of an unhealthy organism as internal asymmetrical organs in many species does not imply malfunction and good genes may be bound both to symmetric or asymmetric phenotypes. Vice versa, some flowers, despite symmetric, deceive pollinators (Schaefer and Ruxton 2009).

The causal link between symmetry and positive stimulus characteristics, when present, is unclear. I suggest that good qualities, virtues, and honesty are part of the meaning associated to of the stimulus and the result of a subjective interpretation; as such, they can change with the observer; conversely, symmetry and other aesthetic canons pertain to the physical structure of the signal. A beautiful structure can be an optimal conditioned stimulus (Guilford and Dawkins 1991). If the observer associates it with the right unconditioned stimulus, a beautiful structure can become an honest predictor of rewards (Wright et al. 2009). In a cooperative context, it is possible to explain a signal both symmetric and honest thanks to the sequential process of perception and associative learning with which pollinators exert a double selection on flowers. However, it must be kept in mind that associative learning captures statistical and not deterministic correlations of the pollinator environment, which cannot, therefore, exclude cases of deception (Benitez-Vieyra et al. 2010).

Conclusions

Aesthetic preference postulated by Darwin to explain beautiful secondary sexual characteristics in mating is a fundamental development in the theory of evolution because it introduces a new type of selection. However, for over a century the explanation of biological beauty has oscillated between Darwin's view based on purposeless aesthetic selection, sometimes maladaptive, and Wallace's beauty conception as an honest advertisement (Prum 2012; Prum 2017). This work, based entirely on experimental data from both naturalistic disciplines and neurosciences, offers a theory that reconciles the two conflicting positions about biological beauty.

Darwin's idea of an aesthetic choice in co-evolutive relationships is correct. The focus on the flower-pollinator system highlights how the beauty of flowers is an emerging property from a recursive process. However, the process is mutually beneficial since it makes flowers conspicuous to pollinators satisfying the need to facilitate their research.

The distinction between the physical structure of the stimulus and its meaning is crucial for correctly defining the beauty canons. In a cooperative context, the beauty canons represent an efficient communication code selected for characteristics of simplicity, invariance, and redundancy, that make them easily identifiable to receiver perception. Favoring a fluent recognition of the stimulus, beauty induces a fast pleasurable emotion in the observer, indicative of better adaptation, because the recognition of stimuli is adaptive in itself.

In general, beautiful signals are useful to keep in touch, but also to avoid each other in cases where it is preferable. As in any message, the meaning is independent of the language used to convey it. This assumption explains why a signal is attractive for one specie and warning for another and still beautiful.

On the other hand, even the simple association of beauty and symmetry with good genes, or beauty with honesty, although this seems reasonable, cannot be taken for granted. The learning abilities conferred by the nervous system enable the observer to detect coincidences.

The empirical observations on pollinators show that these animals, visiting the most conspicuous targets, learn to choose those that predict greater rewards, thus favoring the evolution of flowers whose conspicuous appearance is associated with 'generosity' towards pollinators. Beautiful signals easily detected and memorized represent excellent conditioned stimuli i.e. indicators, signs that make the environment more understandable and predictable.

Associative learning is based on statistical and not deterministic correlations. This may explain cases where the stimulus, although beautiful, is misleading. In fact, the hedonic value of beauty is distinct from that of meaning.

Since some fundamental mechanisms that govern fine perception and learning have been widely observed in many species, human included, it follows that the most basic criteria of stimulus preference are widely shared. This may explain our appreciation for flowers, even if human beings did not participate in their evolutionary process. Therefore, the common idea that beauty is of human relevance only is refuted. Beauty is not an elusive construction of the human mind, but a set of empirically verified perceptive rules correlated to sensory and cognitive mechanisms and at least in part common to any nervous system. In this perspective, beauty canons may be part of a general theory of perception and communication.

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