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A universal model of esthetic perception based on the sensory coding of natural stimuli

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ABSTRACT
Philosophers have pointed out that there is a close relation between the esthetics of art and the beauty of natural scenes. Supporting this similarity at the experimental level, we have recently shown that visual art and natural scenes share fractal-like, scale-invariant statistical properties. Moreover, evidence from neurophysiological experiments shows that the visual system uses an efficient (sparse) code to process optimally the statistical properties of natural stimuli. In the present work, a hypothetical model of esthetic perception is described that combines both lines of evidence. Specifically, it is proposed that an artist creates a work of art so that it induces a specific resonant state in the visual system. This resonant state is thought to be based on the adaptation of the visual system to natural scenes. The proposed model is universal and predicts that all human beings share the same general concept of esthetic judgment. The model implies that esthetic perception, like the coding of natural stimuli, depends on stimulus form rather than content, depends on higher-order statistics of the stimuli, and is non-intuitive to cognitive introspection. The model accommodates the central tenet of neuroesthetic theory that esthetic perception reflects fundamental functional properties of the nervous system.

KEYWORDS: art, esthetics, efficient coding, sparse coding, resonance

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The purpose of this theoretical essay is to outline a universal biological model of esthetic perception. It consists of six chapters. Chapter 1 gives an overview of the interdisciplinary background of esthetics and describes the quest for a universal biological model of esthetic perception. In Chapter 2, prevailing models of vision and their potential relevance for esthetic perception are reviewed. Chapter 3 summarizes recent experimental results demonstrating similarities between the statistical properties of visual art and natural scenes. Based on these experimental findings, I propose a hypothetical model of esthetic perception in Chapter 4. This model is based on the efficient (sparse) coding of sensory input. In Chapter 5, a number of salient characteristics, which are shared by esthetic perception and efficient coding, are discussed. Several experimental implications and testable predictions are derived from the model in Chapter 6.

Chapter 1. *The quest for a universal biological theory of esthetic perception*

Esthetic experience is fundamental to human existence. Philosophers, art historians, art theoreticians, psychologists, art critics and artists alike have been searching for the essence of esthetic experience for centuries. Recently, neuroscientists have joined the search and argued that esthetics is linked tightly to perception (Livingstone, 1988; Gregory *et al.*, 1995; Werner and Ratliff, 1999; Zeki, 1999a, b; Livingstone, 2002). Perception, in turn, is mediated by the sensory organs and the brain. The link between esthetic experience and neural function has been emphasized, in particular, for the visual arts, which are the primary focus of the presented work.

The emerging field of research that deals with the biological basis of esthetics is called neuroesthetics. The central tenet of neuroesthetic theory is that esthetic experience is a product of brain function (Zeki, 1999a, b). A similar idea that esthetic judgment has a biological (physiological) foundation was advanced by the philosopher Edmund Burke (1757). More recently, Gregor Paul (1988) maintained that biological hypotheses are imperative for any explanation of universal esthetic judgment. Furthermore, according to work published in the area of philosophical esthetics, humans are thought to share the same general concept of esthetic judgment (Burke, 1757; Hume, 1757; Kant, 1790; Schelling, 1907; Adorno, 1970; Paul, 1988). Consequently, esthetic judgment is thought to reflect principles that are independent of the cultural, historic, social or personal circumstances, under which a work of art is created. This classic view of universal esthetics is diametrically opposed to contemporary theories of art, which argue that art should be explained in its historic and social context (Goodman, 1968; Danto, 1981).

As a result of research carried out over the last century, much is known about the biological foundations of vision and perception. During the first half of the 20th century, the study of visual perception resulted in the definition of the laws of human vision (for reviews, see Wurtz and Kandel, 2000b; Reid, 2003). During the second half of the 20th century, these laws have been related to the function of nerve cells and of specialized (visual) regions of the brain. It is clear that, for an object of visual art to be appreciated, its optical image has to be projected onto the observer's retina. The retinal image is converted into the activity of an array of photoreceptors. Neural activity is conveyed along specific neuronal channels to higher visual centers in the brain, for example to the visual cortex, where the different dimensions of visual information (for example, contrast, color, or movement) are processed and visual experience reaches consciousness (for reviews, see Wurtz and Kandel, 2000a, c; Reid, 2003).

During the last decades, there has been a lively exchange between artists and visual scientists on visual processes and phenomena. More or less consciously, artists applied scientific knowledge on visual perception to produce special visual effects in their work. Likewise, visual scientists have analyzed works of art and revealed how different styles of art relate to particular aspects of visual information processing (Livingstone, 1988; Rentschler *et al.*, 1988; Gregory *et al.*, 1995; Werner and Ratliff, 1999; Zeki, 1999b; Cavanagh, 2005) or higher (cognitive) visual functions of the brain (Ramachandran and Hirstein, 1999). A comprehensive review of such theories has been published in three issues of the *Journal of Consciousness Studies* entitled "Art and the brain" (edited by the late J. A. Goguen and E. Myin; 1999, 2000, 2004). However, some of the theories proposed to date have been criticized, mainly because each theory applies only to a restricted number of art styles and may not hold for other styles.

Along another line of biological research, called evolutionary or Darwinian esthetics, it has been asked what the function of beauty might be in the evolutionary context. For example, the role of visual characters displayed in the face or on the body of animals or the role of songs produced by birds and insects were studied with respect to mate preference, sexual selection, the assessment of the health and genetic quality in mate choice, and the resulting reproductive success (for reviews, see Grammer *et al.*, 2003; Voland and Grammer, 2003). Evolutionary esthetics contributes to our knowledge on the origin of esthetic perception, and some of the conclusions reached in this type of research apply also to humans, for example in the context of face perception and sexual preference. Nevertheless, the creation and appreciation of art does not seem to have any straightforward advantage for the reproductive success of the artist or the art lover in human societies. Aspects of esthetics that do not relate to reproductive success must therefore also be considered.

A general scientific theory, which explains the biological foundation of esthetic judgment, is lacking to date. The challenge is to find a theory that can be applied as broadly as possible to diverse styles of art. Ideally, such a theory should be as universal as esthetic judgment itself. It should be applicable to works of art as diverse as, for example, the bust of an Egyptian mummy, an Arabic book illustration, Chinese calligraphy, art of native African people, an engraving by Dürer or Rembrandt, and abstract oil paintings by Kandinsky or Pollock. Any universal theory must be independent of factors that vary between different styles, even if the factors determine the characteristic appearance of individual pieces of art. The variable factors may include aspects of the cultural, historical and social background, in which an art object was created, the technique used by the artist, the artist's preference for figurative or constructive elements (dots, lines, objects, shades, people, natural scenes, size and format of the work of art, usage of perspective cues, etc.) or his or her preference for particular aspects of visual processing (color, contrast, motion, etc.). Art historians, art critics, psychologists and neuroscientists have investigated these factors in detail; there are a vast number of books and review articles summarizing their results. To review the variable factors of artistic creation is beyond the scope of this essay. However, being variable, these factors cannot be relevant in the search for a universal theory of esthetic experience.

Chapter 2. *Models of vision and their relevance for esthetic perception*

During the last fifty years, major advances have been made in our understanding how visual objects are encoded by neuronal activity in the vertebrate visual system. At the beginning of this research, neurophysiological studies have focused on the processing of isolated, artificial, and simple stimuli such as local brightness contrast, small circular or elongated objects, their orientations or color, or the motion of small objects (for reviews, see Wurtz and Kandel, 2000a, c; Reid, 2003). Such small stimuli represent the local (first-order) statistics of visual scenes. Generally, local stimuli are presented in the classic receptive field of visual neurons during neurophysiological experiments. The classic receptive field is defined as the area, in which a single neuron can be readily and reproducibly driven by direct stimulation with simple stimuli. At subcortical stages of visual processing and in the primary visual cortex, the classic receptive fields of single visual neurons represent only a small area of the entire visual field. Art objects, however, are usually viewed so that they project to a relatively large region of the visual field. Moreover, the esthetic effect of an individual feature in an art object is usually appreciated in the context of the entire work (see below). As a consequence, the appreciation of art objects is likely to require the activation of areas larger than the classic receptive field or the interaction between neural activities induced by multiple classic receptive fields. For this reason, it is unlikely that studies on the classic receptive field structure of single neurons can elucidate the neuronal correlate of esthetic perception. Rather, higher-order statistics, i.e. more global features encompassing most or all of the art object, must be considered.

Another line of research has revealed that there are different channels in the visual system that process separately the diverse modalities of visual information (for example, contrast, color, motion, spatial frequencies). Moreover, beyond the primary visual cortex, there are multiple discrete cortical regions, which each process specific aspects of the visual scene. Besides regions that process more general aspects of visual information, such as motion and color, there are also highly specialized areas (for reviews, see Wurtz and Kandel, 2000a; Reid, 2003). An example for such a specialized area is a brain region, in which neurons are activated by the presentation of human faces (Perrett *et al.*, 1982; Gross, 2005). Presumably, the neuronal correlate of esthetic perception is not a singular process restricted to any of these higher visual regions or to any specific visual channel because almost any type of visual stimulus can be used to compose esthetically pleasing objects. It is more likely that esthetic perception is mediated in many (if not all) of the different channels and regions of the visual system. As a consequence, esthetic perception probably relates to general aspects of information processing that are implemented in all visual channels.

Nevertheless, much has been learned from studies of visual channels and regions and their relation to different styles of art. Visual scientists have shown that artists are aware of the rules governing visual perception and that they exploit - consciously or unconsciously - these rules in their art (see, for example, Livingstone, 1988; Rentschler *et al.*, 1988; Gregory *et al.*, 1995; Zeki, 1999b; Livingstone, 2002; Van Tonder *et al.*, 2002; Cavanagh, 2005).

At a more fundamental level, Zeki (1999a, b) proposed that esthetics is a product of the brain and must obey its rules. According to his theory on art, it is the task of the artist to represent in painting only the constant and essential elements of an object by extracting the invariant essential characteristics of the objects only from the ever-changing visual world; it is these constancies that allow the brain to obtain knowledge about the world.

Ramachandran and Hirstein (1999) proposed an even more cognitive model of art that is based on eight principles. One of these principles, which is central to their model, is a psychological phenomenon called the peak shift effect, which denotes the exaggeration of salient features that distinguish a given object of interest from other objects. This effect is also the basis of caricatures. In their model, art is thought to be composed according to the peak shift principle and is reinforced by other neural mechanisms such as perceptual grouping, in order to optimally stimulate particular visual areas of the brain. Moreover, art is most appealing if it produces heightened activity by supernormal stimuli along a single dimension rather than in multiple visual modules (for a critical appraisal of this model, see Mangan, 1999; Gombrich, 2000).

In the present work, I shall present a specific hypothesis of how a universal theory of visual esthetic perception can be reached. The model that I propose is based on more fundamental properties of information processing than previous neurobiological theories of esthetics (Ramachandran and Hirstein, 1999; Zeki, 1999b) and, as a consequence, the model proposed here can be applied to a wider range of artistic styles. Nevertheless, even the present model does not embrace all styles of art. Notably, in some styles of contemporary art, artists and art critics consider esthetic appeal insignificant and esthetic appeal may indeed be negligible. Instead, this "non-esthetic" art emphasizes aspects of social sciences, psychology, philosophy, or other aspects relating to human cognition (for example, see Goodman, 1968; Danto, 1981). The visual depiction of these aspects often (but not always, see Paul, 1985) fails to induce esthetic feelings in the observer. In the present work, I reflect only on works of art that have an esthetic appeal, irrespective of the intention of the artist. By doing so, I do not refute the existence of "non-esthetic" art.

Chapter 3. *Scale-invariant (fractal-like) properties of visual art and their relation to natural scenes*

Artists and philosophers alike have argued that the esthetic value of art objects depends on the coherent and harmonious arrangement of the individual visual elements and features that make up the composition (Burke, 1757; Nietzsche, 1888; Matisse, 1908; Kandinsky, 1914; Paul, 1988). Consequently, the esthetic effect of an individual feature in an art object has to be appreciated in the context of other visual features surrounding it. I refer to this dependency as "contextuality". In psychological studies at the beginning of the 20th century, the global structure of visual objects has been defined as a set of rules of "Gestalt". Interestingly, there is a close correlation between some Gestalt rules, which are used to recognize objects based on the grouping of elements in the visual scene, and the structure of natural scenes (Sigman *et al.*, 2001). Several philosophers have invoked the Gestalt character of beauty to explain the esthetically pleasing form of art objects (Kant, 1790; Leibniz, 1873; Nietzsche, 1888; Paul, 1988).

The principle of contextuality is of great importance during the process of creating a work of art. The elements of an art object are put together ("composed") clearly in a non-random fashion. They are arranged in a precise way so that each element relates to most, if not all, other elements in the object. During the creation process, the possibilities of variation are large at the beginning. As the art object approaches its completion, the degree of freedom for making changes and additions decreases. At the end of the creation process, each part of the art object is embedded in the structural context of the entire object and no part can be removed, or changed substantially, without endangering the esthetic appeal of the overall object. The esthetic appeal of an art object depends exactly on how the visual elements or features, which make up the object, are arranged with respect to one another.

In image analysis, local features are referred to as the first-order structure and more global features as its second-order or higher-order structure. One widespread approach to study higher-order structure in visual stimuli is, for example, to analyze their Fourier power spectra. The Fourier spectra of natural scenes exhibit characteristic and uniform properties (Burton and Moorhead, 1987; Field, 1987; Tolhurst *et al.*, 1992; Ruderman and Bialek, 1994). Specifically, the Fourier power falls with the spatial frequency *f* by approximately $1/f^2$ for most natural scenes, although there is variability between individual images (for reviews, see Olshausen and Field, 1996, 2000; Simoncelli and Olshausen, 2001). This statistical property is thought to reflect the scale invariance of natural scenes and it relates to the fractal-like structure of many signals found in the natural environment. Scale invariance implies that, as one zooms in and out of a natural scene, the amount of structure present in the image and its Fourier spectral composition remains the same over a wide range of zooming.

Several philosophers have pointed out that natural beauty and the beauty of art objects share esthetic qualities (Kant, 1790; Hegel, 1833; Adorno, 1970; Paul, 1988, 1998; Koppe, 2004). Because both natural scenes and visual art can be perceived as esthetically pleasing, we recently asked whether the two types of visual stimuli share common higher-order statistical properties. Fourier spectra were measured in a large set of graphic art from the Western hemisphere, ranging from 15th century engravings to 20th century abstract art (see elsewhere in this issue; Redies et al., 2007). Results show that works of art and natural scenes display a similar degree of scale invariance and fractal-like properties. In contrast, three other sets of stimuli with little or no esthetic appeal (photographs of laboratory and household objects, plants and parts of plants, and scientific illustrations) were found to display significantly different Fourier power spectra, which indicated that most of these images were not scale-invariant. This result implies that artists create art with statistical properties that are not necessarily the same as those of the subject depicted. Rather, artists adjust the image statistics of their subjects during the process of creation so that, in their works of art, statistics are more similar to those encountered in complex natural scenes. Interestingly, within the sample of graphic art analyzed, cultural variables, such as techniques, centuries and country of origin, and subject matters, had no prominent effect on the general scaling properties. This independence from cultural variables suggested that scale invariance might be a universal property of visual art (Redies et al., 2007). However, it remains to be established whether other forms of Western art and art from of cultures display also scale-invariant properties.

In this context, it should be pointed out that fractal properties have been discovered previously in the abstract drip paintings of the artist Jackson Pollock (Taylor *et al.*, 1999; Taylor, 2002). Jackson Pollock created his works before Benoit Mandelbrot described fractals for the first time (Mandelbrot, 1975). The fractal properties of Pollock's paintings are not merely a result of his dripping technique because paintings by inexperienced and naive subjects using the same dripping technique are not fractal (Taylor, 2002). Richard Taylor and his colleagues subsequently showed that humans display a consistent preference across fractal images, with a peak esthetic preference for a fractal dimension in the range of 1.3-1.5 (Spehar *et al.*, 2003; Taylor *et al.*, 2005b).

Fractal-like image properties may be necessary, but they are not sufficient to induce esthetic perception for several reasons (Redies et al., 2007). First, images with fractal-like properties, which have been generated by computer programs, look strikingly natural, but they have relatively low or no esthetic value (Ruderman, 1997; Lee and Mumford, 1999; Olshausen and Field, 2000). Similarly, there are examples of images depicting real and natural objects that display fractal-like structure but they are not necessarily esthetically pleasing. Also, the esthetic perception induced by art objects is usually more intense than that induced by natural scenes, suggesting that there are additional factors that have an effect on esthetic perception or are prerequisites for esthetic perception, as postulated by philosophers (Kant, 1790; Hegel, 1833; Schelling, 1907; Adorno, 1970; Koppe, 2004) (see Section 5.5). Last but not least, in the statistical analysis described above, Fourier power spectra are measured by radially averaging the amplitudes of each frequency in the Fourier plot. In this procedure, information on the orientation of the frequencies in the image and their phase is lost. These factors, however, are likely to have an important effect on image structure and esthetic appearance.

The experimental results summarized in this chapter have lead to the suggestion that the biology of esthetic perception is related to the coding of natural stimuli in the visual system (Redies et al., 2007). In the following chapter, I will take up this suggestion and outline a general and universal theory of esthetic perception.

Chapter 4. ***A universal model of esthetic perception based on the sparse (efficient) coding of sensory input***

In recent years, visual scientists have investigated neuronal responses to stimuli that extend beyond the classic receptive fields of single neurons and cover relatively large areas of the retina and visual field. By doing so, they have studied how individual visual features are perceived in relation to surrounding features. Note that it is this more global stimulation of the retina that occurs under normal vision. Strikingly, the responses of single visual neurons to entire visual scenes are often reduced ("sparsified") when compared to responses of the same cells to the type of more localized and simple stimuli that were used in earlier neurophysiological studies (Vinje and Gallant, 2002). Sparse coding implies that the responses by pairs of neurons become strongly decorrelated (Vinje and Gallant, 2000). A general result from these studies is that sensory input is encoded in an efficient manner in the visual system ("efficient" coding), both at low and higher levels of visual information processing. This means that, out of a large population, relatively few neurons are active simultaneously ("population sparseness") or that the responses of neurons over time are reduced ("lifetime sparseness") (Olshausen and Field, 2004). The theory of efficient coding goes back to an idea of Horace Barlow who hypothesized that the role of early (low-level) sensory neurons is to remove statistical redundancy from the sensory input (Barlow, 1961). By coding sensory information efficiently, the overall neural activity to a visual stimulus is decreased, allowing a more economical use of metabolic resources in the nervous system (Balasubramanian and Berry, 2002; Lennie, 2003).

Another important result from these studies is that maximally efficient coding is observed for complex natural stimuli, to which the sensory systems are adapted during evolution, development and adaptation. The theory of sparse cording is supported by theoretical, physiological and computational evidence obtained by several groups during the last decade. Excellent reviews on this subject have been published (Sekuler and Bennett, 2001; Simoncelli and Olshausen, 2001; Hoyer and Hyvärinen, 2002; Simoncelli, 2003; Olshausen and Field, 2004).

Efficient coding is rooted in neural mechanisms, which are intrinsic to the nervous system and have been adapted during the evolution of the human species and the development of the individual; they are also subject to behavioral modifications and adaptations (Sekuler and Bennett, 2001; Hoyer and Hyvärinen, 2002; Lewicki, 2002; Simoncelli, 2003; Olshausen and Field, 2004; Sharpee *et al.*, 2006; Smith and Lewicki, 2006). It is clear that the neuronal machinery, which results from this adaptation process, does not respond to all stimuli in the same way. For example, stimuli that are grouped coherently into objects elicit less activity at lower levels of visual information processing when compared to random stimuli (Murray *et al.*, 2002). Since the visual responses are adapted optimally to the processing of natural scenes, the neural networks respond to them in a specific way (Sekuler and Bennett, 2001), like the string of a musical instrument that resonates to particular frequencies. In a similar way, esthetically pleasing objects may induce a specific state of activity (or lack of activity) in the observer.

I here propose that an artist strives to create a composition that is able to put his own nervous system into a particular functional state (resonance). In order to achieve this goal, the artist constantly compares and adjusts the object being created with an inner visual representation of this functional state. If the artist is successful, she or he produces a coherent ensemble of visual elements that can induce the specific neural state in the artist's own nervous system. It is this state which represents the neurophysiological correlate of esthetic perception. In a similar context, the artist Wassily Kandinsky used the term "vibration in the human soul" for the process of creating a work of art (Kandinsky, 1914). In this sense, works of art reflect basic brain functions (Zeki, 1999b); the human brain thus resonates to esthetic stimuli that reflect these properties. A similar idea has been advanced by Richard Taylor and his colleagues for the perception of fractals in the drip-paintings by Jackson Pollock and in other fractal displays (see above, Taylor *et al.*, 2005a). Also, the mechanism of "resonant" adaptation has been used in self-organizing neural networks simulating sensory coding. These networks can explain a wide range of perceptual processes in vision and the other senses ("adaptive resonance theory, [ART]") (Grossberg, 1976b, 1980; Grossberg and Mingolla, 1985).

In view of the observed similarities in image statistics between visual art and natural scenes (see Chapter 3), I propose that esthetic perception is based on the same neuronal mechanisms that underlie efficient (sparse) coding of sensory inputs. As outlined above, the artist creates a visual stimulus ensemble that is characterized by scale-invariant properties. I hypothesize that the resonant state, which this stimulus can evoke in the brain, relates to the adaptation of the visual system to natural scenes. In other words, the artist adapts his art to the visual system that, in turn, is adapted to the natural environment. Consequently, it should be possible to describe the resonant state induced by esthetic stimuli in terms of the efficient coding paradigm.

Supposing that adaptive resonance is a universal and general perceptual mechanism (Grossberg, 1976a, 1980; Grossberg and Mingolla, 1985), the neural state induced by esthetic stimuli should be a specific type or particular degree of resonance in the sensory systems. For example, it is conceivable that the retinal image of an art object can be processed by the visual system with maximum efficiency. This could mean, for example, that the visual responses to an art object are sparsified to a minimum, or that visual art is represented in the visual system in a particularly efficient way in single neurons (lifetime sparseness). Furthermore, art objects may induce specific patterns of neural activation in the visual system, for example an evenly distributed activation across the entire ensembles of neurons. Another possibility would be that the responses of neurons are highly similar (or dissimilar) across the neuronal population or that they are maximally sparse across the entire population (population sparseness).

It is possible that the resonant neural state is reflected also in additional nervous system properties, like response synchronization in local neural networks. For example, esthetic stimuli may elicit maximally synchronous or asynchronous neuronal responses in the nervous system

(Averbeck and Lee, 2004; Roelfsema *et al.*, 2004; Bichot *et al.*, 2005; Wang, 2005).

In conclusion, esthetic qualities may not be fundamentally different from general sensory qualities, but probably differ in the degree or specific distribution of the neural activity, which they elicit in the brain. This hypothesis may explain why sensory stimuli can be more or less esthetic, with a continuous transition between esthetic and non-esthetic stimuli, depending on the degree of neural resonance that a particular stimulus can induce.

Chapter 5. *Salient characteristics shared between esthetic perception and sensory coding*

The efficient coding hypothesis of esthetic perception remains to be proven experimentally and should be considered a working hypothesis at present. However, there are a number of characteristics shared between esthetic perception and sensory coding. They are discussed in the present chapter. These similarities suggest, but do not prove, that the two phenomena might indeed be related. Some of the points made here about art are suppositions that have been advanced by artists, philosophers or art historians. These suppositions lack a basis in natural sciences and must therefore be considered intuitive and speculative for the most part, at least with regard to strict biological reasoning. Because the suppositions may not find universal approval, it is important to state them clearly in order to point out the restricted validity of any conclusions drawn from them.

5.1 *Esthetic perception is a function of form rather than of content.* The idea that esthetic judgments are based on the form rather than on the content of art objects has been advanced by several philosophers (Burke, 1757; Kant, 1790; Wilde, 1890; Paul, 1988; Goguen, 2000). Amongst these philosophers, there is general consensus that the pleasure derived from esthetic perception differs from emotional sensations like erotic feelings or disgust. Notably, it has been argued that ugly or disgusting things can also be depicted in an esthetic way (Rosenkranz, 1893). This consensus is also reflected in the terms introduced by philosophers to characterize sensations related to esthetic perception (for example, "uninterested pleasure", Kant, 1790; discussed in Paul, 1988).

Moreover, abstract (non-representational) art, which by definition is devoid of any semantic meaning or any content that can be expressed readily in every-day language, can also be esthetic. Artists of the last century, such as Kandinsky, Mondrian and Pollock, shifted gradually from representational art to abstract art during their careers, suggesting that the two types of art share fundamental similarities, at least for the artists (Kandinsky, 1935; Mondrian, 1937). Abstract art is included in the present considerations and represents a particular challenge, but perhaps a genuine opportunity. Abstract art calls for a neural explanation of esthetics that is strictly based on the structure and the arrangement of individual pictorial elements and is not based on its content because content is absent in abstract art. Even for figurative art, it is clear that its content is highly variable between different styles of art and thus cannot serve to deduce universal principles of esthetics.

The efficient coding model is a formal paradigm that helps to understand how the structural information contained in visual stimuli, that is their form, is processed in the nervous system. The efficient coding model does not take into account any processing relating to the content of the stimuli and largely excludes top-down (cognitive) mechanisms of information processing. In this regard, it represents a neuronal paradigm suitable to accommodate the perception of esthetic form.

5.2 *Esthetic principles are obscure to basic human cognition and language.* The content depicted in figurative art objects can be analyzed by cognition or expressed by language. In contrast, the universal principles of esthetics seem to be inaccessible to human introspection and discordant with basic cognition and every-day language. In fact, they have escaped definition so far. It has even been argued that the neuronal processes underlying esthetic perception remain unconscious and that this unconscious processing might be the reason why esthetic perception is obscure to cognition (Mangan, 1999; Goguen, 2000). Most artists, however, strive (sub-)consciously for a very specific pictorial structure or form when they create a work of art. Some (sub-)conscious decision-making must therefore take place during this creation process, even if the rationale behind the esthetic decisions remains outside the realm of human cognitive introspection.

The same introspective inaccessibility pertains to efficient coding. Although the principles of efficient coding can be formulated readily in mathematical and physiological terms, the neuronal mechanisms underlying efficient coding remain largely obscure to basic human introspection and cognition. This is underlined by the fact that efficient coding in the nervous system has been discovered only recently.

5.3 *Esthetic perception correlates with a neuronal state of similar nature in all observers ("universality").* Western philosophers postulated the existence of universally valid criteria for esthetic judgment (Burke, 1757; Kant, 1790; Hegel, 1833; Schelling, 1907; Adorno, 1970; Paul, 1988), as did non-Western philosophers (for a review, see Paul, 1985). Accordingly, a work of art has the potential of inducing esthetic perception in human observers independent of the circumstances of its creation. In turn, every human can potentially appreciate the esthetics of works of art from all periods, cultures and styles (see also Kandinsky, 1912). Esthetic perception is thought to be as universal in humans as, for example, the perception of colors or emotions like happiness or anger. I will refer to this supposition as the "universality assumption".

At the surface, the universality assumption runs against the fact that the appreciation of art depends significantly on cultural, social, historic and other factors, which relate to the content depicted in the art object as well as to its form. In general, human beings tend to favor art objects they are familiar with. Unfamiliar art is often rejected, for example art created according to a novel style, or art from alien cultures or another social group. In the history of art, many novel styles of art have shocked the public and infuriated art critics. In several complex ways, art and its esthetic evaluation are adapted and restricted to features that are important for a particular culture or society (Thornhill, 2003). The apparent contradiction between this cultural dependence of art appreciation and the universality assumption can be solved if one assumes that familiarity is a prerequisite for esthetic perception rather than its cause. As outlined by the ethologist Eibl-Eibesfeld, art objects convey cultural content and, by doing so, they enhance the social bonding between individuals in a group (Eibl-Eibesfeldt, 1988). This social function of esthetic perception, however, should not be confused with its biological basis. Familiarity acts like a cultural filter, which can allow or block appreciation of art by the individual in a given culture. The presence of cultural filters, however, does not preclude the existence of universally valid rules of esthetics. The vast amount of literature on the history and psychology of art testifies that the cultural filters can be immensely complex. It is beyond the scope of the present essay on the sensory coding of art to give an overview of the reception of art in different cultures and societies.

This is the subject of art history, art theory and the psychology of art.

Efficient coding is a universal general principle underlying information processing in the nervous system. It is not restricted to specific channels of visual information processing or to any specific sensory modalities (vision, audition, olfaction and sensation). Efficient coding has been demonstrated in several species, including invertebrates (Schwartz and Simoncelli, 2001; Hahnloser *et al.*, 2002; Laurent, 2002; Lewicki, 2002; DeWeese *et al.*, 2003; Theunissen, 2003; Olshausen and Field, 2004; Machens *et al.*, 2005; Sharpee *et al.*, 2006). It is independent of any cognitive, cultural, social, historical or other factors that might be presented in different visual stimuli perceived by human subjects. Because of this independence from variable factors of esthetic stimuli, it is well suited to account for the universality of esthetic perception.

5.4 *The esthetic perception elicited by the beauty of natural objects is similar to that induced by art objects.* For centuries, artists have depicted objects or scenes from nature in their art, including landscapes, flowers, the human body or their own faces. They are inspired by the esthetic appeal of natural objects and try to enhance their esthetic attributes in their creations. As already discussed above, Western and non-Western philosophers have pointed out that the beauty of art and nature share common underlying features (Kant, 1790; Hegel, 1833; Adorno, 1970; Paul, 1988, 1998; Koppe, 2004). The relation between the esthetic qualities of natural things and art is one of the central issues of philosophical esthetics. There is general agreement that natural subjects are not *per se* beautiful and that art objects can be esthetic without depicting natural things. Consequently, mere imitation of nature cannot be considered art and esthetic art has qualities superior to or different from natural beauty (Kant, 1790; Hegel, 1833; Schelling, 1907; Adorno, 1970; Goguen, 2000; Koppe, 2004). Nevertheless, any biological theory of art must accommodate the fact that natural forms can elicit esthetic feelings that are related, in some fundamental way, to the feelings induced by esthetic works of art.

The model based on efficient coding offers a straightforward explanation of why natural scenes are often considered beautiful. If esthetically pleasing objects elicit a neuronal response in the visual system similar to that induced by natural scenes, the two types of stimuli must be perceived in a similar way. This similarity in perception justifies the usage of a similar set of descriptive terms (for example, "beautiful") for both types of stimuli. At the same time, the model can also explain the differences between art and nature (see following section).

This part of the model is testable in neurophysiological experiments. By recording neuronal activity from visual centers of higher mammals, the responses of single neurons to aesthetic stimuli can be compared to those of natural scenes or more simple stimuli, both by stimulating the classic receptive field alone and together with its surroundings (non-classic receptive field). If the model is correct, neuronal responses should be sparsified (or synchronized) when esthetic stimuli are presented in the non-classic receptive field.

5.5 *Difference between beauty of natural scenes and art objects*

Works of art depicting natural scenes or objects are usually not mere copies of their natural counterparts (Kant, 1790; Hegel, 1833; Schelling, 1907; Adorno, 1970; Goguen, 2000; Koppe, 2004). If natural objects induced esthetic feelings in the same way as art, it would not be necessary to create art objects. Vice versa, there are esthetically pleasing works of art that do not depict natural things. What then is the difference between the esthetics of natural beauty and art objects?

As discussed by Simoncelli and Olshausen (2001) in the context of efficient coding, nervous system function depends not only on the environment but also on intrinsic factors of the nervous system, like its computational capabilities and the functional limitations of neurons. Efficient coding paradigms emphasize the influence of the environment, but neglect the intrinsic factors, which regulate the wiring of neural networks during development and contribute to nervous system plasticity. The intrinsic factors represent biological properties of the nervous system. For example, the molecular mechanisms of pattern formation and morphogenesis that govern the development of neural circuits are very similar to those underlying the formation of other organs or organisms. Not surprisingly, when the morphology of nerve cells is visualized, their elaborate arborizations can display esthetic qualities, as do other natural objects. In conclusion, the visual neural networks are not only adapted to natural scenes, but they are also related closely to the laws of nature at the level of intrinsic neural properties.

A work of art is created through constant feedback with the artist's visual system so that a specific state of neural activity is induced. As a result, art objects reflect not only the higher-order statistical properties of natural scenes, to which the visual system is adapted (Chapter 3), but also intrinsic properties of the visual system. I hypothesize that this additional reflection of intrinsic properties distinguishes art objects from natural scenes. Implicit to this hypothesis, the visual system can resonate more profoundly to art objects than to natural scenes. In other words, esthetic art can be tuned more precisely to nervous system properties than natural scenes are. This prediction can also be tested in neurophysiological experiments that study differences in visual responses to natural scenes and works of art, for example in their degree of sparseness.

A similar difference between the average statistics of natural stimuli and artificial stimuli, which the sensory system is optimized for, has been demonstrated recently in the auditory system of the grasshopper (Machens *et al.*, 2005). The optimal stimuli largely overlap with a behaviorally important subset of natural sounds. These results indicate that the coding strategy of sensory neurons is not matched to the statistics of natural stimuli *per se*, but is influenced also by other factors, such as behavioral relevance among natural stimuli, which may have co-evolved with the intrinsic neural mechanisms during evolution (Machens *et al.*, 2005). Whether a similar influence also exists for the human visual system is an open question. For example, behaviorally relevant stimuli for the visual system are human faces and their emotional expressions. Interestingly, the criteria for the judgment of facial beauty seem to be universal amongst human subjects, also in different cultures (for review, see Rhodes, 2006).

Chapter 6. *Implications of the model and open questions*

In this chapter, I will discuss several issues that arise from the efficient coding model of esthetic perception and their implications for experiments in the field of neuroesthetics.

6.1 *Efficient coding: a common theory for all sensory modalities?*

Although the present considerations are focused on visual esthetics, the efficient coding model of esthetics can also be applied to other senses, in particular to the auditory system, in which efficient coding mechanisms have also been demonstrated (Theunissen *et al.*, 2001; Lewicki, 2002; Olshausen and O'Connor, 2002; Machens *et al.*, 2005; Smith and Lewicki, 2006). A general validity has been postulated also for the mechanism of adaptive resonance implemented in neural networks that can explain different kinds of perception (Grossberg, 1987).

As far as audition is concerned, much has been learned in recent years about the diverse brain regions and neural networks underlying music production and perception (for reviews, see Koelsch and Siebel, 2005; Peretz and Zatorre, 2005). Being non-representational for the most part, abstract rules, such as harmony, have been considered as the basis of music for centuries. However, many of the formal rules of composition have changed over time and do not represent universals. Universally valid principles of composition have yet to be discovered. One notable exception is the (cross-cultural) observation that music is performed according to a steady beat; if tempi change during the performance, they relate to each other by means of low order integral ratios (1:2, 2:3, 3:4, or the inverse) (Epstein, 1988).

A recent study revealed that response properties recorded from the cat auditory nerve closely match a representation of natural sounds that is predicted by a sparse coding model of auditory processing of the same stimuli. The same match is also found for speech suggesting that speech evolved to match efficient coding in the auditory system (Smith and Lewicki, 2006). It would be feasible to extend this type of analysis to the perception of music. Interestingly, scale-invariant, fractal-like properties have also been found in examples of classical music (Hsu and Hsu, 1990; 1991).

6.2 *Is esthetic perception restricted to the human species?*

I have argued that esthetics is based on a general principle of neural function. If this is correct, esthetic perception should not be restricted to the human species, but animals should also be able to appreciate beauty and perhaps even produce esthetically pleasing patterns. For example, in the auditory domain, it would be of interest to study whether the song of birds and of higher mammals like whales displays higher-order statistics that can be related to the coding of sensory stimuli in these animals. One distinct aspect of human music, the horizontally transmitted change of its content and structure between individuals over time, has been observed also for the song of whales (Rendell and Whitehead, 2001; Mercado *et al.*, 2005). Moreover, the neural sequences underlying the generation of song in a songbird are based on an ultra sparse code (Hahnloser *et al.*, 2002). The authors recorded neural activity from the song-generating (high vocal) center (HVC) of zebra finches. They demonstrated that individual HVC neurons discharge at a single, precise time during a neuronal sequence relating to song production, with different HVC neurons busting sequentially with respect to one another. These results indicate that not only the perception but also the production of esthetic tonal structures may be based on efficient coding. In summary, it is conceivable that efficient coding is also the basis of esthetics in the animal kingdom.

Efficient coding is a principle that has been demonstrated in the nervous system of many vertebrate and invertebrate species. The idea that the principles underlying esthetics and efficient coding are related, might possibly answer the question why there are examples of cross-species appreciation of esthetic patterns. For example, some songs produced by birds are attractive not only to their gender mates but also to humans. An example for cross-species esthetic judgment in the visual domain are the elaborate plumage patterns displayed by some birds to attract their sexual partners (see, for example, McGraw *et al.*, 2002). Humans consider the same patterns beautiful. Any statistical properties shared between esthetic and natural stimuli should thus also be present to some degree in stimuli that animals find attractive. However, it should be noted that most patterns displayed by one species are not attractive to other species *per se*, as is also true for artistic displays by humans in different cultures. Cultural filters that preclude esthetic perception (see above) may also exist in animals and possibly prevent cross-species appreciation of most esthetic stimuli that are directed towards members of the same species.

A distinction must be made between the ability to perceive and appreciate beauty and the ability to create art. Clearly, an art critic, who has never learned and will not learn to use a painting brush or a pencil, cannot be turned into an artist. The creation of visual art requires technical, cognitive and perhaps also cultural capabilities that mankind acquired only relatively recently, when cave art appeared about 30.000 years ago. Hence, the production of complex works of art, at least in the visual domain, is largely restricted to the human species. As pointed out, however, it is conceivable that the song generated by some animals has esthetic qualities. If the efficient coding model of esthetic perception is valid, esthetic perception might have originated in the animal kingdom following the implementation of efficient coding mechanisms in neural networks. Consequently, esthetics might be a phenomenon that is less recent in evolution and more closely linked to the biology of the nervous system than thought previously (see also Grammer *et al.*, 2003). When precisely we can speak of esthetics in animal behavior will be a question of definition. The biological function of beauty and attractiveness in animals is a current focus of behavioral research and beyond the scope of the present review. It seems likely, however, that the biological function of esthetics played a more important role earlier in evolution than in modern human society.

6.3 *Implications for functional imaging studies*

The recent advent of functional brain mapping technologies, like functional magnetic resonance tomography (fMRT), has allowed investigating the localization of brain regions activated by different sensory stimuli, motor performance or mental activity. fMRT studies have contributed greatly to our knowledge of regional brain function. Two recent fMRT studies described the responses of human subjects to visual stimuli that were considered beautiful. Jacobson and coworkers (2006) demonstrated that esthetic judgment of beauty of geometrical shapes relies on a network in the brain that also underlies evaluative judgments on social and moral cues. Kawabata and Zeki (2004) demonstrated a differential regional responsiveness of the orbito-frontal and motor cortices to different categories of figurative and abstract art that were considered either beautiful or ugly. The orbito-frontal cortex is involved also in response to other stimuli that are emotionally rewarding. As pointed out by the authors, fMRT does not detect those areas that are involved in a particular task but are not activated (Kawabata and Zeki, 2004). If esthetic perception correlates to a sparsification of neural responses, then the areas involved in this response may indeed escape detection by fMRT because their overall activity remains low (see, for example, Murray *et al.*, 2002). Moreover, emotional responses that are a consequence of the perception of esthetic objects in a given individual may confound the picture (for example, see Lang *et al.*, 1998; O'Doherty *et al.*, 2003), as can the reaction to the content of the images and cultural attitudes of the subjects towards the images (cultural filter). Just consider the classic question of whether an esthetically pleasing work of art can be created by depicting an ugly toad. Assuming that esthetic form and content conveyed by art objects are separate entities (Section 5.1), the answer is clearly affirmative (Rosenkranz, 1893; Paul, 1988). The subjects viewing such a work of art may have an emotional reaction to the ugliness of the toad, which should not be confused with any neural responses that correlate with the esthetic qualities of the work. It will therefore be important in future imaging studies to precisely distinguish and map independently the responses to the esthetic, emotional and cultural aspects of visual art in the human brain.

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