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Art and brain coevolution

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Abstract

The competence for appreciating beauty appears to be a human universal trait. This fact points out to a phylogenetically derived capacity that, somehow, evolved by means of natural selection. To detail how this evolutionary process took place is difficult to determine, because appreciating beauty is an elusive capacity, impossible to be detected in the fossil record. However, efforts have been made to understand the main characteristics of such competence, particularly by means of the advances of neuroaesthetics. Here, we examine some of the results obtained in experimental research to identify neural correlations of the appreciation of beauty, as well as archaeological and paleoanthropological proofs of the relationship existing between production of artistic objects and evolution of the human brain.

Keywords: Coevolution; Neuroaesthetics; Beauty; Artistic objects; Human brain; Neural correlates

The capacity for appreciating aesthetic qualities in objects, movements, and sounds seems to be a human universal; all human groups have such competence.

The capacity for *producing* aesthetic items is also universal: painters, dancers, and musicians are not restricted to any culture or historical epoch. However, *appreciating* aesthetic attributes—what we may call “beauty”—goes beyond producing them in at least two aspects. First, “artists” (producers) make up a small fraction of human groups; on the contrary, “spectators” are numerous. Second, it is possible to appreciate aesthetic qualities in natural objects and events, such as sunsets on a beach, whales’ songs, or flights of birds. These natural aesthetic items have no author.

We cannot establish the phylogenetic appearance of the human competence for appreciating beauty. Neither fossil nor archaeological records contain evidences enough to ascertain the appearance of such capacity. It is not possible to ascertain whether spectators with ability enough for appreciating landscapes, dances, or songs did exist in previous human species.

Producing beauty seems less elusive, though its origin is also difficult to establish. Regarding artworks, Paleolithic polychromies, for instance, are too developed an example of the presence of artisans. Some traces of early artists’ work should exist. How can we detect them?

In a previous work ([Cela-Conde and Ayala, 2007](#)), we have extensively examined early evidences of decorative, artistic, or symbolic object. We will not repeat again the arguments in favor of the eventually symbolic condition of burials, for instance. Since we are now interested in the coevolution of art and the brain, we will change the focus, searching for items of proof of mental correlates that might speak in favor of a capacity for appreciating beauty.

1 Neuroaesthetics

Beyond some valuable precedents, such as Ramachandran and Zeki’s ideas on art and the brain, the empirical field of neuroaesthetics started in 2004, when three different studies offered the first accounts of the activation of brain areas during aesthetic appreciation. Vartanian and Goel found brain activity related to preference for artworks in the right caudate nucleus, the left cingulate sulcus, and the bilateral fusiform gyri ([Vartanian and Goel, 2004](#)). Kawabata and Zeki identified activity in the medial orbitofrontal cortex (OFC) for Beautiful, compared with Ugly, stimuli, and also in the anterior cingulate gyrus in Beautiful vs Neutral stimuli ([Kawabata and Zeki, 2004](#)). In turn, Cela-Conde and collaborators found increased activity for Beautiful stimuli, compared with Not-beautiful, in the left prefrontal dorsolateral cortex ([Cela-Conde et al., 2004](#)).

Since 2004, many related investigations have been published. Due to the different cognitive tasks asked of the participants, a large part of the brain has been identified as activated when aesthetic appreciation occurs (see [Table 1](#)).

Table 1 Brain Areas Activated in 20 Neuroaesthetics Experiments

alt-text: Table 1

Area	N	Cognitive Processes
vMPFC: ventromedial prefrontal cortex	1	Resting state
aMPC: anterior medial prefrontal cortex	5	
pCC: posterior cingulate cortex (L left, R right)	1	
Precuneus	2	
SN: substantia nigra	1	Reward and emotional processing
Hippocampus	5	
DS: dorsal striatum (caudate)	3	
VS (Nacc): ventral striatum (nucleus accumbens)	4	
Amygdala	2	
Insula	4	
ACC: anterior cingulate cortex	6	
OFC: orbitofrontal cortex	5	
Temp P: temporal pole	3	
DLPFC: dorsolateral prefrontal cortex	3	
VLPFC: ventrolateral prefrontal cortex	4	
Motor C: motor cortex	4	Perceptual processing
Occip C: occipital cortex	8	
P. hippo C: parahippocampal cortex	1	
TPJ: temporoparietal junction	1	
SPC: superior parietal cortex	2	
IPC: inferior parietal cortex.	2	

The column “N” expresses the number of experiments mentioning each brain area.

Some early models of the cognitive activity of appreciation of beauty exist. [Chatterjee \(2003\)](#) indicates the existence of a temporal sequence of processing within the nervous system. [Chatterjee's \(2003\)](#) model distinguishes between early, universal, and late, personal, stages of aesthetic perception. The point of departure is the visual attributes of the object whose perception is performed similarly as perceptions otherwise unrelated to aesthetic appreciation. By means of a binding process, forms, colors, and spatial arrangements of movements—if any—are combined engaging frontal-parietal circuits. These neural networks inherent to the attention lead, through a feedforward system, to further processing of different attributes including mnemonic domains related to previous personal history (places, faces). An emotional component adds hedonic sensations by extending the feedforward system. The complete phenomenon integrates what might be called the universal, innate components of visual perception (including the limits of the psychophysical as perceivable wavelengths) and the subjective aspects that relate to past experience of the subject (including its historical and cultural context) ([Fig. 1](#)).

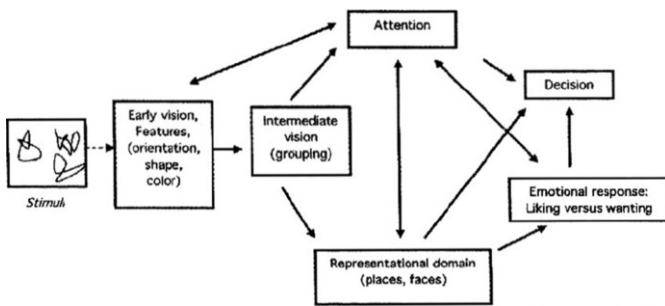


Fig. 1 Chatterjee's (2003) model of the neural underpinnings of visual aesthetics.

alt-text: Fig. 1

The model of Leder et al. (2004) provides a frame sequential process which considers the same elements as Chatterjee's (2003) scheme, but with some important additions. Aesthetic judgment is now included within the aesthetic experience per se. Crucial features of the context of perception are taken into account (to see an object in a museum is not the same as seeing it in the street or in a private home). Also, the training experience of the subject (expert/nonexpert) forms part of the model (Fig. 2).

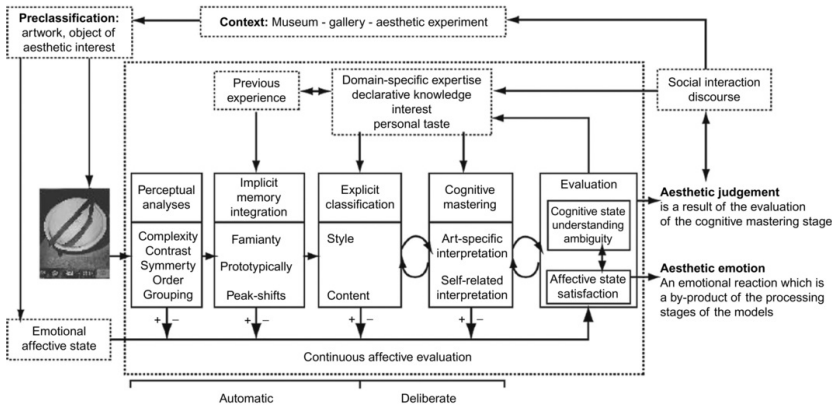


Fig. 2 Leder et al.'s. (2004) model of aesthetic appreciation and aesthetic judgment.

alt-text: Fig. 2

2 Neural Networks

Chatterjee's (2003) and Leder et al.'s (2004) models theoretically imply the existence of connectivity among the different brain areas related to the perception of beauty, i.e., the activity of neural networks.

Regarding aesthetics networks, Brown and collaborators proposed the existence of a "core circuit for aesthetic processing" by means of a model in which exteroceptive information passing through the OFC, and interoceptive information passing through the anterior insula, are integrated to achieve aesthetic appraisal (Brown et al., 2011). However, this model is not based on any empirical studies of aesthetic appreciation. Rather, it is grounded in analyses of the reward system and valence processing.

Empirical verification of neural connectivity has also been addressed. The most interesting contribution with respect to putative aesthetic networks may have been the suggestion advanced by Jacobsen et al. (2006) and Vessel et al. (2012) of connections between medial parts of the frontal cortex (FMC), the precuneus (PCUN), and the posterior cingulate cortex (PCC) among other regions (see list in Table 2). These interconnected areas coincide in part with what is known as the default mode network (DMN).

Table 2 Regions Active Under Aesthetic Perception, Corresponding Brodmann Areas, and Talairach Coordinates

alt-text: Table 2

		BA Area	Talairach Coordinates			A	B
Frontomedial cortex	FMC	10	1	54	26	x	
Anterior medial prefrontal cortex	aMPFC	10	− 6	38	4		x
precuneus	PCUN	7	− 4	− 47	32	x	x
Posterior cingulate cortex	PCC	23/31	1	− 18	41	x	
Left posterior cingulate cortex	PCC	23/31	− 9	− 49	18		x
Superior frontal gyrus	SFG	10	22	45	26	x	
Frontomedial/anterior cingulate	FMC/AC	9/32	1	23	32	x	
Left inferior frontal gyrus	lIFG	44/45/47	− 46	17	0	x	
Right inferior frontal gyrus	rIFG		46	24	0	x	
Left temporal pole	ITP	38	− 43	2	− 29	x	
Right temporoparietal junction	rTPJ	39/40/42	46	− 56	32	x	
Left temporoparietal junction	lTPJ		− 41	− 59	35	x	
Superior frontal gyrus	SFG	6	− 5	19	62		x
Left substantia nigra	SN		18	− 12	− 6		x
Left hippocampus	HC		− 30	− 21	− 10		x

After (A) [Jacobsen et al. \(2006\)](#) and (B) [Vessel et al. \(2012\)](#). Neither one of these articles includes analyses of functional connectivity.

Activation of the DMN during aesthetic perception seems surprising. This network was identified by Raichle and collaborators as a baseline state of the brain present under resting conditions and being curtailed when some concrete action is performed ([Fox et al., 2005](#); [Raichle et al., 2001](#)). Aesthetic judgment is a task of such concrete kind. [Jacobsen et al. \(2006\)](#) instructed participants to rate visual stimuli in order to answer the question “Is this pattern beautiful?” comparing the obtained results with those of a second question: “Is this pattern symmetric?” In turn, [Vessel et al.’s \(2012\)](#) asked participants to rate visual stimuli on a one- to four-scale answering the question “how strongly does this painting move you?” Thus, in both studies, concrete cognitive processes demanding attention were implied. At least those of: (i) seeing stimuli, (ii) appreciating their aesthetic content, (iii) rating it, and (iv) formulating the result as aesthetic judgment.

2.1 Why DNM Remains Activated in Neuroaesthetics Experiments?

The answer to this question requires exploring the characteristics of neural connectivity. Holding that one neural network is formed when performing a cognitive task leads to the assumption that some kind of connection exists between the implied areas. The notion of connectivity has been largely considered by anatomists, neurologists, and psychologists to be at the core of explanations of consciousness. Following [von der Malsburg and Schneider \(1986\)](#), connectivity is associated with the presumed synchronization of neuronal assemblies—synchronous “firing.” Eventually, distributed local networks of neurons would be transiently linked by reciprocal dynamic connections ([Varela et al., 2001](#)).

3 Functional Connectivity

Statistical studies on the synchrony of firing can identify the existence of a “functional connectivity” of brain areas ([Friston et al., 1993, 1995](#)) defined as the statistically temporal dependency of neuronal activation patterns of anatomically separated brain regions ([van den Heuvel and Hulshoff Pol, 2010](#)). Using functional connectivity to hypothesize the existence of neural networks is a common procedure. In order to obtain such connectivity, temporal series of activation/deactivation of presumably synchronized neurons must be compared. As it is well-known, such temporal series can be obtained by means of functional magnetic resonance imaging (fMRI). This technique detects changes

in blood oxygen content in brain areas—what, following [Ogawa et al. \(1990\)](#), is called blood oxygen level-dependent (BOLD) signals—due to activity along a determinate span of time.

Combining temporal series of BOLD signals and advanced statistical means of analysis like graph methods, brain architecture consisting of modules of neural functional connectivity can be determined. A review of the literature on the resting-state functional architecture carried out by [Lee et al. \(2012\)](#) reported the identification of seven networks. Apart from the DMN, these networks correspond to different particular processes ranging from relatively simple perception to higher cognitive achievements. [Fig. 3](#) shows the correspondence between He et al.'s (2009) modules and cognitive systems.

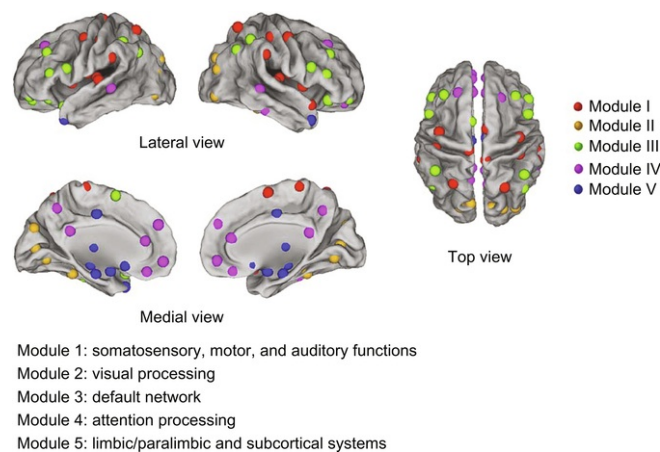


Fig. 3 Association between modules and cognitive systems (He et al., 2009).

alt-text: Fig. 3

Recent publications have conveyed the need to investigate the aesthetic perception by identifying the functional networks that become thereby activated ([Boccia et al., 2016](#); [Marcus et al., 2016](#); [Nadal, 2013](#)). The identification of such networks, however, faces a major problem related to the features of the available techniques for determining the temporal series of neuronal activation.

If the cognitive process, whose neural correlate is searched for, keeps its activity during a considerable span of time, fMRI is an accurate technique to obtain connectivity patterns. However, compared with the relatively stable condition of subjects' brain activity during resting state, aesthetic perception refers to cognitive processes taking place in a much shorter time ([Cela-Conde et al., 2004](#)). Variations of BOLD signals along several seconds are not accurate enough to detect such changes, since networks might be modified in a relatively narrow time during aesthetic processing tasks. Some studies have focused dynamic changes in brain networks using fMRI techniques ([Bassett et al., 2011](#)), but their time windows cover several minutes. Therefore, to reach brain activation related to the perception of beauty it is mandatory to use high temporal resolution techniques, like electroencephalography (EEG) or magnetoencephalography (MEG).

EEG and MEG have high temporal resolution, but less spatial resolution; for fMRI the reciprocal is the case. We are thus facing a methodological dilemma. Either (i) we choose to determine with a high spatial resolution the distribution of active modules in the brain, but only promediating a large period of time, or (ii) we choose to detect dynamic changes in short time spans, but just obtaining the modular structure of the cortical surface.

The time span involved in the aesthetic perception—slightly over 1 s, as we shall see—does not allow the identification by means of fMRI registers of the neuronal networks that become activated. The reviews of neuroaesthetics referenced earlier ([Boccia et al., 2016](#); [Marcus et al., 2016](#); [Nadal, 2013](#)) do not include any results concerning the functional connectivity obtained by fMRI. Although they record an investigation of the dynamics of brain networks in the aesthetic appreciation, obtained by means of MEG ([Cela-Conde et al., 2013](#)). The authors obtained temporal series of brain activity for 24 participants during resting state and judgment of beauty of 400 diverse visual stimuli. Then, they estimated the synchronization in the beta band of the temporal series by means of Pearson correlation coefficient and phase-locking value ([Mormann, 2000](#); [Pereda et al., 2006](#)). The MEG signals were split into three temporal windows ([Fig. 4, top](#)):

- TW0, 500 ms (milliseconds) prior to stimuli projection
- TW1, 250–750 ms after stimuli projection
- TW2, 1000–1500 ms after stimuli projection

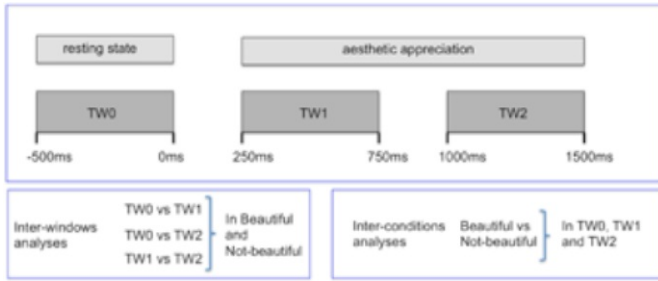


Fig. 4 Temporal windows and conditions compared in the analysis of brain dynamics during aesthetic appreciation (Cela-Conde et al., 2013).

alt-text: Fig. 4

Interwindow comparisons evaluated the differences in connectivity between temporal windows along each condition. Intercondition comparisons evaluated differences in connectivity between Beautiful and Not-beautiful stimuli in each temporal window (Fig. 4, bottom).

Cela-Conde et al.'s (2013) results show that the neural connectivity present in the resting state is curtailed in the first temporal window (TW1; Fig. 5, top), being replaced by what the authors call the "initial aesthetic network." This network mainly connects occipital regions (Fig. 5, middle).

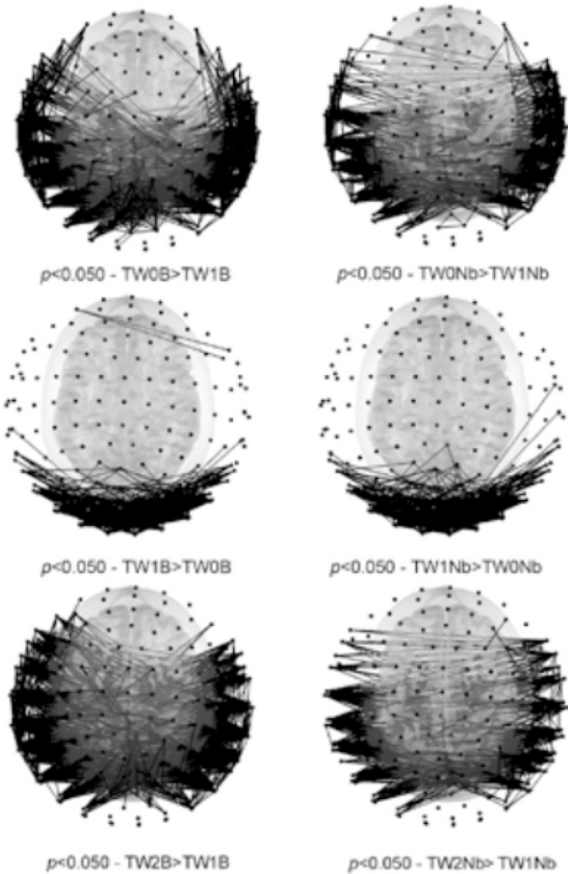


Fig. 5 Differences in synchronization before Beautiful (*left*) and Not-beautiful (*right*) stimuli. *Top*: TW1 > TW0. *Bottom*: TW2 > TW1 (Cela-Conde et al., 2013).

alt-text: Fig. 5

The initial aesthetic network is nearly the same before Beautiful and Not-beautiful stimuli. However, during the second temporal window (TW2) significant differences depending on the judgment of beauty appear. The “delayed aesthetic network” identified in Cela-Conde et al.’s (2013) experiment consists of synchronized activity mainly present along medial occipital, lateral occipital, lateral posterior parietal, medial parietal, medial frontal, and dorsolateral prefrontal in the left hemisphere, as well as in the right lateral parietal (Fig. 5, bottom).

The dynamic scenario during aesthetic appreciation seems to be, thus, as follows:

- i. a starting point of high synchronization during the resting state (TW0);
- ii. this connectivity is curtailed during the TW1, and being replaced by a different network;
- iii. part of the resting-state networks is later recovered during the TW2.

Both Beautiful and Not-beautiful conditions share, during the TW2, a bilateral higher synchronization along frontal-parietal-temporal-occipital lateral regions. This pattern matches the similar bilateral synchronization during the resting state. Due to its lateral position, this connectivity would have little relationship with the medially placed DMN. Hypothetically speaking, it is sound to hold that attentional tasks, obviously engaged in the aesthetic appreciation, would be responsible for this network.

In turn, differences of synchronization in favor of Beautiful stimuli mainly affect medial parts of the brain. These differences are better shown in the TW2 intercondition analysis, which manifests that a higher connectivity exists in favor of the Beautiful stimuli (Table 3 and Fig. 6, left). Not-beautiful stimuli do not show any higher synchronized link (Table 3 and Fig. 6, right).

Table 3 Number of MEG Sensors and Links More Synchronized in the Intercondition Comparisons at $P < 0.050$

alt-text: Table 3

	Beautiful > Not-Beautiful		Not-Beautiful > Beautiful	
	Sensors	Links	Sensors	Links
TW0	6	3	0	0
TW1	2	1	0	0
TW2	19	10	0	0

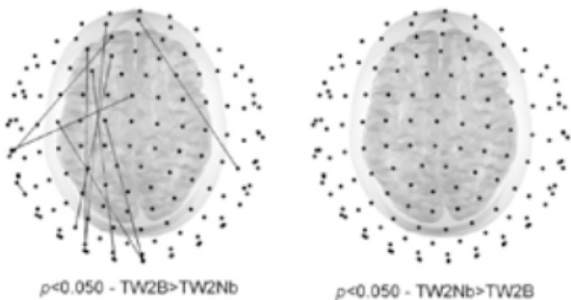


Fig. 6 Intercondition comparison in the second temporal window (TW2). *Left*, higher synchronization for Beautiful stimuli. *Right*: higher synchronization for Not-beautiful stimuli.

alt-text: Fig. 6

We are confronting the delayed aesthetic network. Fig. 7 shows it from different perspectives.

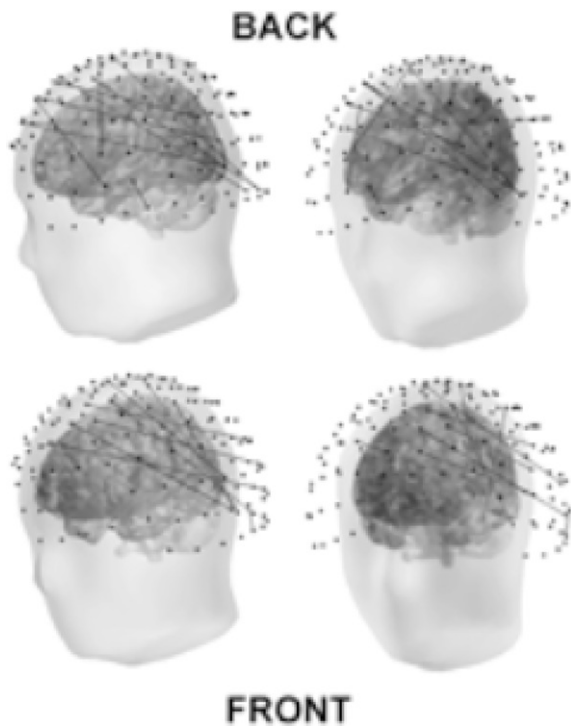


Fig. 7 The delayed aesthetic network from different perspectives.

alt-text: Fig. 7

The delayed aesthetic network matches, in part at least, the DMN of the resting state. As we will see, this coincidence may throw some light on the elusive question of the evolution of the human aesthetic capacity.

4 Perceiving Beauty as a Human Trait

Neuroaesthetics experiments have been normally carried out with very specific groups of subjects: college students from developed countries in most cases. However, aesthetics, i.e., artworks, are distributed globally, impinging on people able to recognize products of other cultures as artworks. This universality is, in the opinion of [Carroll \(2004\)](#), an argument in favor of considering that art may serve universal adaptive purposes.

Theoretically speaking, a trait can be universal because it has been inherited from an ancestor who fixed it—plesiomorphy—thus being shared with other species belonging to the human lineage. Alternatively, we may consider that the trait was developed as a new feature—apomorphy—quite early in our species. In this second case, all modern humans would have the capacity for appreciating beauty, but no other species would share this trait. However, this universality poses a problem. As it is well-known, brain tissues are metabolically expensive. Resting-state activity likely accounts for the major cost, in terms of energy, of running the brain ([Raichle, 2011](#)). In the awake resting state, the brain accounts for 20% of the total oxygen consumption of the body, despite the fact that it represents only 2% of body weight ([Gusnard and Raichle, 2001](#)). It is difficult to justify how any brain-related capacity would have become fixed during human evolution without explaining its benefits ([Aiello and Wheeler, 1995](#)). The adaptive advantages of aesthetic appreciation remain to be accounted for—though a different possibility, considering it as an exaptation, exists; we will examine it later.

The power of artworks to build communities of sentiments, promoting the cohesion of groups, seems a conspicuous advantage ([Dissanayake, 1992, 2007](#)). Aesthetics would be a cohesion factor, thus adaptively convenient. Also, the emotional, i.e., hedonic reward of art offers an explanation for the eventual selection of the capacity for appreciating beauty (for instance, [Dutton, 2003](#)). Both reward and cohesion factors are good hypotheses to account for the current relationships existing between beauty and art ([Dissanayake, 2009](#)). What to say about their evolutionary journey?

Though, as we have said, the phylogenetic appearance of the brain correlates for appreciating beauty cannot be ascertained, producing beauty seems less elusive. Works of art and decorative objects persist after the disappearance of their creators. Since painters' or sculptors' works are durable, but dancing movements and music sounds are not, we will hence forward refer only to objects as artworks when speaking of the evolution of the human

aesthetic capacity.

4.1 When Did This Capacity Appear?

Though “beauty,” “art,” and “aesthetics” are different concepts that might be even in opposition—consider, for example, the movement known as “Ugly Art”—we will take these three concepts as equivalent. A cautionary note must be stated. Since natural objects can be considered as beautiful by spectators too, the capacity for appreciating beauty might be much more previous in time and extended in space than actual artistic objects produced with purpose of being aesthetically moving. In a similar manner, some spectators could consider as “beautiful” an object—a lithic tool, for instance—manufactured for practical purposes.

The lack of correspondence between artists’ intentions and spectators’ responses is well-known, with many examples present in the recent history of art. Some examples are the popular reaction before the first Impressionists’ exhibitions, or the initial reception of the Eiffel Tower. Therefore, the current consideration of lithic tools, or of any other object, as “beautiful” is not a proof of either the purpose of the artisans that produced them or the eventual aesthetic appreciation of the spectators at that time. Having this caution in mind, authors dealing with the phylogeny of aesthetics distinguish between objects that can be used as tools, like handaxes, and objects that do not have any “practical” benefit—thus, “symbolic”—such as decorative objects.

To deny the usefulness of decorative objects is obviously excessive: it is apparent that such objects convey, for example, social status. Also, other symbolic activities, such as music or dancing, may be useful to emphasize the integration of a social group (Gamble, 2012; Zaidel, 2018). Such behaviors leave no residue in the archaeological record, except by means of pictorial representations (Christensen et al., 2017) or musical instruments (Conard et al., 2009). However, these are recent evidences, namely, posterior to the arrival of *Homo sapiens* in Europe, although there may be other doubtful examples somewhat previous (Atema, 2014). But, if we leave aside the roles of social expression and refer to practical use in a strict sense, as it is the case for lithic tools, the symbolic criterion becomes useful. Nonpractical objects belonging to the archaeological record are items of proof pointing to the appearance of aesthetic appreciation.

A long controversy between archaeologists, paleontologists, and anthropologists refers to the question of whether Neandertals had the capacity for manufacturing artworks. Some Neandertal sites contain decorative objects; for instance, the Grotte du Renne (Arcy-sur-Cure, France) has yielded a series of up to 36 objects, such as carved ivory pieces and perforated bones, the sole purpose of which must have been decorative (Hublin et al., 1996). Hublin et al. (1996) interpreted the Arcy-sur-Cure artifacts as the result of cultural exchange. d’Errico et al. (1998) arrived at a different conclusion: those objects were the result of an independent and characteristically Neandertal cultural development, which had managed to cross the threshold of the symbolism inherent in decorative objects. White (2001) has offered an alternative interpretation: “It seems implausible that [...] Neandertals and Cro-Magnons independently and simultaneously invented personal ornaments manufactured from the same raw materials and using precisely the same techniques.” Consequently, White defended that the Châtelperronian ornaments from the Grotte du Renne are Aurignacian and were produced by modern humans.

In addition to Arcy-sur-Cure, two other Neandertal sites have provided perforated shells: Cueva de los Aviones (genus *Acanthocardia*, *Glycimeris*, and *Spondylus*, with rests of colored pigments into the shell in the latest case) and Cueva Antón (genus *Pecten*), both in Murcia (Spain) (Zilhão et al., 2010).

4.2 Had Neandertals Reached This Cognitive Level?

Dating of paintings found in Altamira, El Castillo, and Tito Bustillo caves (Spain) suggested ages as old as 35.6/40.8 thousand years for several artistic-like symbols and marks (Pike et al., 2012). This considerable age could even be carried further back in time, perhaps by thousands of years (Appenzeller, 2013). If it is so, arguments in favor of considering Neandertals’ decorative items as a mere copy from similar objects manufactured by modern humans cannot be longer held. Our species would not have reached southern Europe by that time.

Whether Neandertals discovered decorative objects by themselves, or they imitated the manufacture and use from modern humans is not easy to determine. Some proofs of cultural sharing during the early Upper Paleolithic exist. Karavanic and Smith (1998) documented the presence of two contemporary sites at Hrvatsko Zagorje (Croatia) which are close to each other. The Vindija Cave has yielded Neandertals, while Velika Pécina has only produced remains of anatomically modern humans. The authors believe that the coincidences exhibited by the tools from both sites are due to imitation or even commercial exchange. These Croatian sites do not include ornaments, but they provide remarkable indications of cultural exchange. Nevertheless, the cognitive capacity linked to perception of beauty does not depend on skills for manufacturing decorative objects. If Neandertals appreciated pendants enough to imitate, stole, or exchange them, it would be beyond doubt that they considered perforated shells and bones to be “beautiful objects.”

5 Patterns of the Evolution of the Brain

If Neandertals and modern humans shared a quite similar capacity for appreciating aesthetic objects, the question would be whether we can link this capacity to Neandertal brain characteristics.

[Bruner et al. \(2003\)](#) analyzed the transition from a generalized archaic pattern of the brain within the genus *Homo* to the modern and Neandertal morphologies. Comparing metric variables and landmark data on physical endocasts and from virtual reconstructions based on computed tomography and 3D image analysis, [Bruner et al. \(2003\)](#) concluded that “archaic and Neandertal specimens share a common endocranial model, in which a large amount of variation is based on a single allometric trend. In this case, encephalization (viewed as cerebral volumetric expansion) structurally influences the variation in endocranial shape. This trajectory represents therefore a continuous gradation, ranging from archaic small specimens [...], to archaic larger ones [...] up to the extremely encephalized Würmian Neandertals.”

The “archaic” pattern shared by Neandertals involves a relative reduction of the length and width of the occipital lobes, a vertical development, an enlargement of the frontal breadth, and the shortening of the parietal chord. The main difference with the modern human pattern of the brain refers to the parietal development of the modern morphotype, something that [Bruner et al. \(2003\)](#) consider that it may have represented “a key to surpass the encephalization constraints imposed by the archaic structural model.”

Expansion of the frontal lobes is an evolutionary trait shared by Neandertals and modern humans ([Bruner and Holloway, 2010](#)). On the other hand, modern humans developed a neomorphic hypertrophy of the parietal volumes, leading to a dorsal growth and ventral flexion (convolution) characteristic of the cranial globularity of our species ([Bruner, 2004](#)).

[Roseman et al. \(2011\)](#) analyzed cranial morphological integration—covariance of traits—in a sample of 2524 modern humans and 20 Neandertals concluding that the overall patterns are significantly different between one and the other species. Nevertheless, Neandertals are consistent with a modern human pattern of integration for more than three quarters of the traits. To what extent these similarities and differences could affect neurological configuration cannot be assessed for the moment.

6 Comparative Studies

Human-derived features may also be distinguished by means of comparative approaches with nonhuman primates.

[Rilling et al. \(2007\)](#) offered a comparison between the brain activation in humans and chimpanzees during the resting state. These authors analyzed, by means of PET, anesthetized chimpanzees that, during the awake resting state, would have completely fixed radioactive glucose in the brain. According to their results, both humans and chimpanzees seem to coincide in the activation of medial and dorsolateral OFC, as well as medial parietal cortex, with the highest level of activity placed more dorsally in humans (BA 9, BA 32) and more ventrally (BA 10) in chimpanzees. As [Rilling et al. \(2007\)](#) held, during the resting state “the strongly left-lateralized activity related to language and conceptual processing in humans was absent in chimpanzees.”

[Watanabe \(2011\)](#) obtained, also by means of PET, the default network curtailed in awake rhesus monkeys when attention-demanding cognitive tasks were performed. [Watanabe \(2011\)](#) shows that “Similar to the human default system, all monkeys showed higher rest-related activity in the medial prefrontal and medial parietal areas (...).” Moreover, considering that the human DMN is related to internal thought processes, Watanabe stated that default activity in the medial brain areas suggests that “there might be internal thought processes in the monkey.”

Mentioning the chimpanzees case, [Northoff and Panksepp \(2008\)](#) assumed that high degrees of self-relatedness correspond to high resting-state neuronal activity. If Watanabe and Northoff and Panksepp are right, the similarities between monkeys, apes, and humans might indicate a self-relatedness capacity, shared in some degree. However, aesthetic capacity does not equal self-relatedness. Probably, the more interesting aspect of the comparative approaches is the strong left-laterality identified by [Rilling et al. \(2007\)](#) as a human trait not present in apes during the resting state. Let us return to the identification between the DMN and the aesthetic networks.

7 Aesthetic Appreciation as an Exaptation

It has been posited that aesthetic perception does not need to imply any adaptive advantage, since it could profit from other previously evolved cognitive characteristics with their own adaptive benefits. In other words, aesthetics might be just an exaptation. For instance, [Kaplan \(1987\)](#) states that “It would be adaptive for animals to like the sort of settings in which they thrive.” Thus, preference for landscapes would have led to preference for ornaments like gardens. Focusing on positive-valence aesthetic appraisal, [Brown et al. \(2011\)](#) hold that “such a system evolved first for the appraisal of objects of survival advantage, such as food sources, and was later coopted in humans for the experience of artworks for the satisfaction of social needs.”

Obviously, any hypothesis about the subject would be difficult to test. However, a complementary justification for the evolution of capacities for appreciating beauty may be given by pointing out the coincidence between the delayed aesthetic network and the DMN.

A fundamental function of the DMN is facilitating responses to stimuli. As [Raichle and Snyder \(2007\)](#) held “intrinsic activity instantiates the maintenance of information for interpreting, responding to and even predicting environmental demands.” This functional capacity seems adaptive enough to justify by itself its metabolic costs, and it is performed by means of “mind-wandering” processes, in which DMN seems to play a fundamental role.

A DMN phylogenetically fixed and linked to aesthetic perception is sufficient to justify such human capacity for appreciating beauty in objects. A different question is that of explaining how this link between DMN and aesthetic perception appeared or, in other words, what characteristic of the DMN might lead to the sudden experiences of the beauty of a picture or a landscape.

An added function of the DMN relates to “mind-wandering” processes. Mind wandering refers to images, thoughts, voices, and feelings that the brain spontaneously produces in the absence of external stimuli (stimulus-independent thoughts, SITs hereafter) (Mason et al., 2007). The SITs are what we might call “the mind talking with itself.”

Three possible explanations of the functional significance of mind wandering were offered by Mason et al. (2007). SITs would enable subjects to maintain an optimal level of arousal. Alternatively, SIT would add coherence to one's experience—past, present. A nonadaptive meaning was also taken into account by these authors. SIT could be a by-product of a general ability to manage concurrent mental tasks obtained during human evolution. Although mind wandering can be useful, “the mind may wander simply because it can” (Mason et al., 2007).

Aesthetic perception is not a SIT. Except in the case of recalling past experiences, detecting beauty depends on external stimuli. However, the aesthetic perception might be a by-product of that general capacity for mind wandering. Mind wandering is a general process of perception neither guided by any goal nor directed to any particular aspect. It obviously applies to the aesthetic appreciation of the environment. According to Kaplan (1987), the step forward from appreciating landscapes to recreate them as artworks is supported by the coincidence between DMN and the aesthetic delayed network.

A close-to-mind-wandering capacity for assigning beauty or ugliness to visual stimuli, from landscapes to artworks, could thus lead to continuous and very quick processes of aesthetic perception. Sudden comprehension that solves a problem or a perceptual ambiguity has been detected, combining EEG and fMRI (Kounios and Beeman, 2009; Kounios et al., 2008), as the culmination of a series of neural processes at different time scales leading to *Aha!* moments. Regarding aesthetic perception, our current study suggests that the appreciation of beauty might be an *Aha!* moment too, which appears at early temporal stages of the perceptive process, and is not guided by goal-directed tasks but working in an almost holistic way. In turn, the obvious advantages of the capacity of beauty appreciation, going from the inner hedonic complacency to the satisfaction of social needs (Brown et al., 2011), would add adaptive advantages to further uses of such a trait. Not surprisingly, aesthetic perception also activates regions, like DLPFC, linked to executive functions (Jacobsen, 2006; Vessel et al., 2012).

8 The Question of Quale

The internal, but stimulus,-dependent visual appreciation of beauty is an individual instance of subjective and conscious experience—what philosophers call “quale” (Lewis, 1929). The intriguing problem of qualia, i.e., the mind-brain relationship, can be stated as follows: How does the brain produce qualitative subjectivity? (Searle, 2011).

In their study of consciousness, Crick and Koch put aside the “hard problem” of quale, the subjective content of the mental states: “no one has produced any plausible explanation on how the experience of redness or red could arise from the actions of the brain” (Crick and Koch, 2003). Instead, Crick and Koch focused on the “soft problem”: the neural correlates of consciousness. Regarding aesthetic appreciation, this “soft problem,” consisting of the localization of brain areas active when subjects gauge the beauty of a visual object, has been already solved, in part at least, by means of neuroaesthetics.

Moreover, some aspects of the dynamics of aesthetic appreciation could help us to scratch the surface of the “hard problem” too. By means of a combination of fMRI, MEG, and behavioral studies of impaired subjects, it seems that the way in which the experience of beauty could arise from the actions of the brain may begin to be within our reach. However, current approaches to the hard problem only yield partial solutions. On the one hand, it seems that the *structure* of the qualia, consisting of a description of mental processes leading to the appreciation of the beauty of an object, can be accessed by means of scientific procedures. On the other hand, many personal circumstances, from previous experiences to character traits, plus health, age, maybe gender, as well as the cultural and historical particularities of each subject and epoch, surely contribute to the experience of appreciating beauty. These aspects would modify, in a still not detailed fashion, the subjective feelings. For the time being, the *content* of the qualia—the eventual result of beauty, or its absence, as an inner sensation—remains out of our reach.

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