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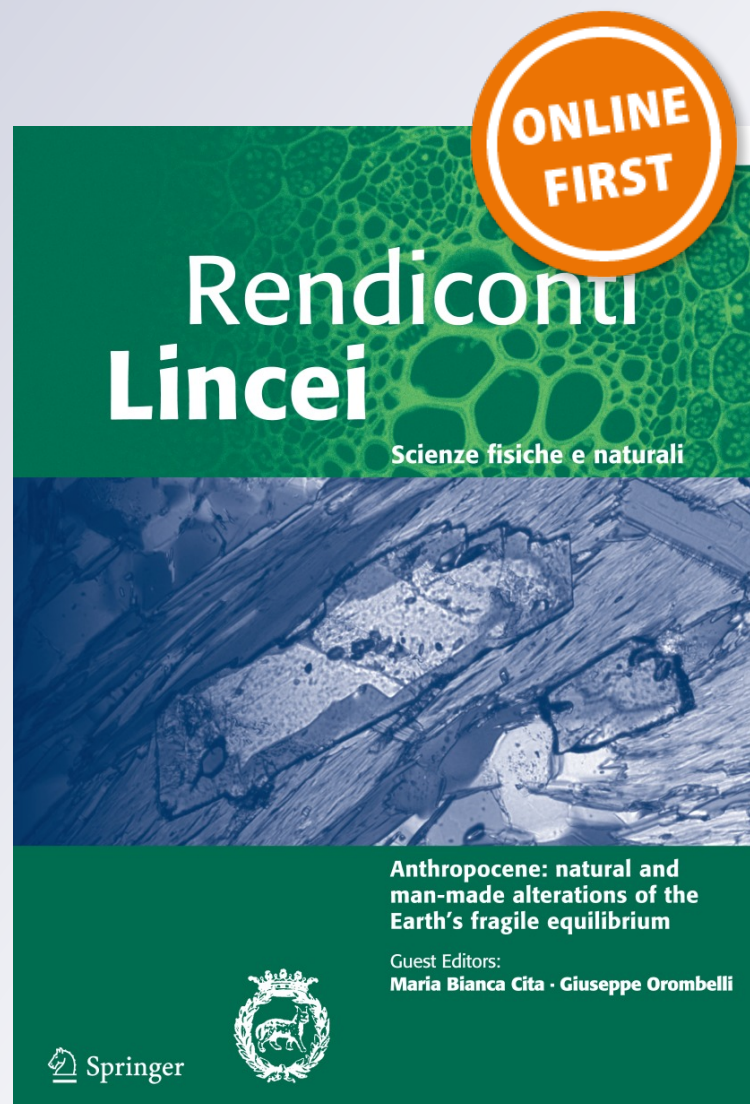
Brain keys in the appreciation of beauty: a tale of two worlds

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Brain keys in the appreciation of beauty: a tale of two worlds

Camilo J. Cela-Conde · Francisco J. Ayala

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Abstract Functional connectivity can be defined as the statistically temporal dependency of neuronal activation patterns of anatomically separated brain regions. The analysis of functional connectivity can lead to brain networks. Here, we report the result of an experiment that has shown two different brain networks related with the appreciation of beauty, corresponding to different time spans in the cognitive processes implied. We describe and discuss such networks, as well as their eventual evolutionary meaning.

Keywords Brain networks · Functional connectivity · Neuroaesthetics · Dynamics

1 Introduction

A Tale of Two Worlds is the title of a Frank Lloyd's silent film released in 1921 and almost forgotten today. Its screenplay tells a story of forbidden love because of the ethnic and cultural barriers that stood then between China and the United States.

This contribution is the written, peer-reviewed version of a paper presented at the Giornata Golgi 2013 "Brain Science and Human Culture", held at the Accademia Nazionale dei Lincei in Rome on June 3, 2013.

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Also, a tale of two worlds is a good metaphor for the barriers standing between the personal, subjective appreciation of beauty and the scientific, objective analysis of brain activity.

Can these two worlds, separated since the philosopher Descartes' times, be joined?

This Golgi Day Conference brings together relevant scientists that have offered crucial keys on the relationships existing between human culture and brain functions. According to their guidelines, in our discussion we will assume the following points:

- Cognitive—'mental'—processes are, from the more simple to the more complex, functional states of the brain
- A functional state of the brain appears when different neural areas are linked, i.e., functionally connected
- Functional connectivity can be defined as the statistically temporal dependency of neuronal activation patterns of anatomically separated brain regions
- The analysis of functional connectivity can lead to brain networks
- The best description available of the brain correlates of cognitive processes consist of such networks, thus far.

Here, we will take for granted these general points, focusing our inputs on the brain networks related with the appreciation of beauty—what is called "neuroaesthetics"—as well as their eventual evolutionary meaning.

2 Neuroaesthetics

Beyond the valuable precedents of 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 account 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 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). The “beautiful” or “not-beautiful” condition of each stimuli was established as the result of the subjective, personal decision of the participants in the experiment. This personal, non-objective, definition of beauty is shared by most publications in the neuroaesthetics field.

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

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 orbitofrontal cortex (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.

The most interesting contribution with respect to putative aesthetic networks may have been the suggestion advanced by Jacobsen and collaborators (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 on Table 2). These interconnected areas coincide in part with what is known as the default mode network (DMN).

Activation of the DMN during aesthetic perception seems surprising. This network was identified by Raichle et al. (2001) as a baseline state of the brain present under resting conditions and being curtailed when some concrete action, like an aesthetic judgment, is performed (Raichle et al. 2001; Fox et al. 2005).

Why DMN remains activated in neuroaesthetics experiments?

In order to obtain an answer, we have recently carried out a study of the dynamics of brain networks in aesthetic appreciation (Cela-Conde et al. 2013). By means of magnetoencephalography (MEG), we obtained temporal series of brain activity for 24 participants during resting state and

Table 1 Brain areas activated in 20 neuroaesthetics experiments

Area	No	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	Judgment and decision making
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 “No” expresses the number of experiments mentioning each brain area

judgment of beauty of 400 diverse visual stimuli. Then, we estimated the synchronization in the beta band of the temporal series by means of Pearson correlation coefficient and phase locking value (PLV) (Mormann 2000; Pereda et al. 2006). The MEG signals were split into three temporal windows (Fig. 1, up):

- TW0, 500 ms (milliseconds) prior to stimuli projection
- TW1, 250–750 ms after stimuli projection
- TW2, 1,000–1,500 ms after stimuli projection

Inter-window comparisons evaluated the differences in connectivity between temporal windows along each condition. Inter-condition comparisons evaluated differences in connectivity between beautiful and not-beautiful stimuli in each temporal window (Fig. 1, bottom).

Our results show that the neural connectivity present in the resting state is curtailed in the first temporal window (TW1; Fig. 2, up), being substituted for what we call the “initial aesthetic network”. This network mainly connects occipital regions (Fig. 2, middle).

The initial aesthetic network is almost the same before beautiful and not-beautiful stimuli. However, during the second temporal window (TW2) significant differences depending on the judgment of beauty appear. What we call the “delayed aesthetic network” 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. 2, bottom).

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

1. A starting point of high synchronization during the resting state (TW0);
2. This connectivity is curtailed during the first temporal window (TW1), and being substituted by a different network;
3. Part of the resting state networks is later recovered during the second temporal window (TW2).

Both beautiful and not-beautiful conditions share, during the second temporal window, 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 inter-condition analysis, which manifest that a higher connectivity exists in favor of the beautiful stimuli (Table 3; Fig. 3, left). Not-beautiful stimuli do not show any higher synchronized link (Table 3; Fig. 3, right).

We are confronting the delayed aesthetic network. Figure 4 shows it from different perspectives.

The delayed aesthetic network matches, in part at least, the default mode network 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.

Table 2 Regions active during aesthetic perception, corresponding to Brodmann areas and Talairach coordinates

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

After (A) Jacobsen et al. (2006), and (B) Vessel et al. (2012). None of these articles included analyses of functional connectivity

Fig. 1 Temporal windows and conditions compared in the analysis of brain dynamics during aesthetic appreciation (Cela-Conde et al. 2013)

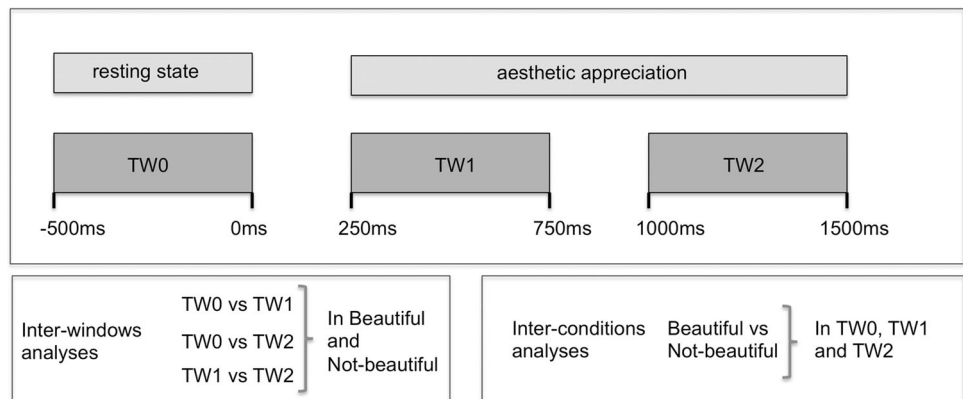
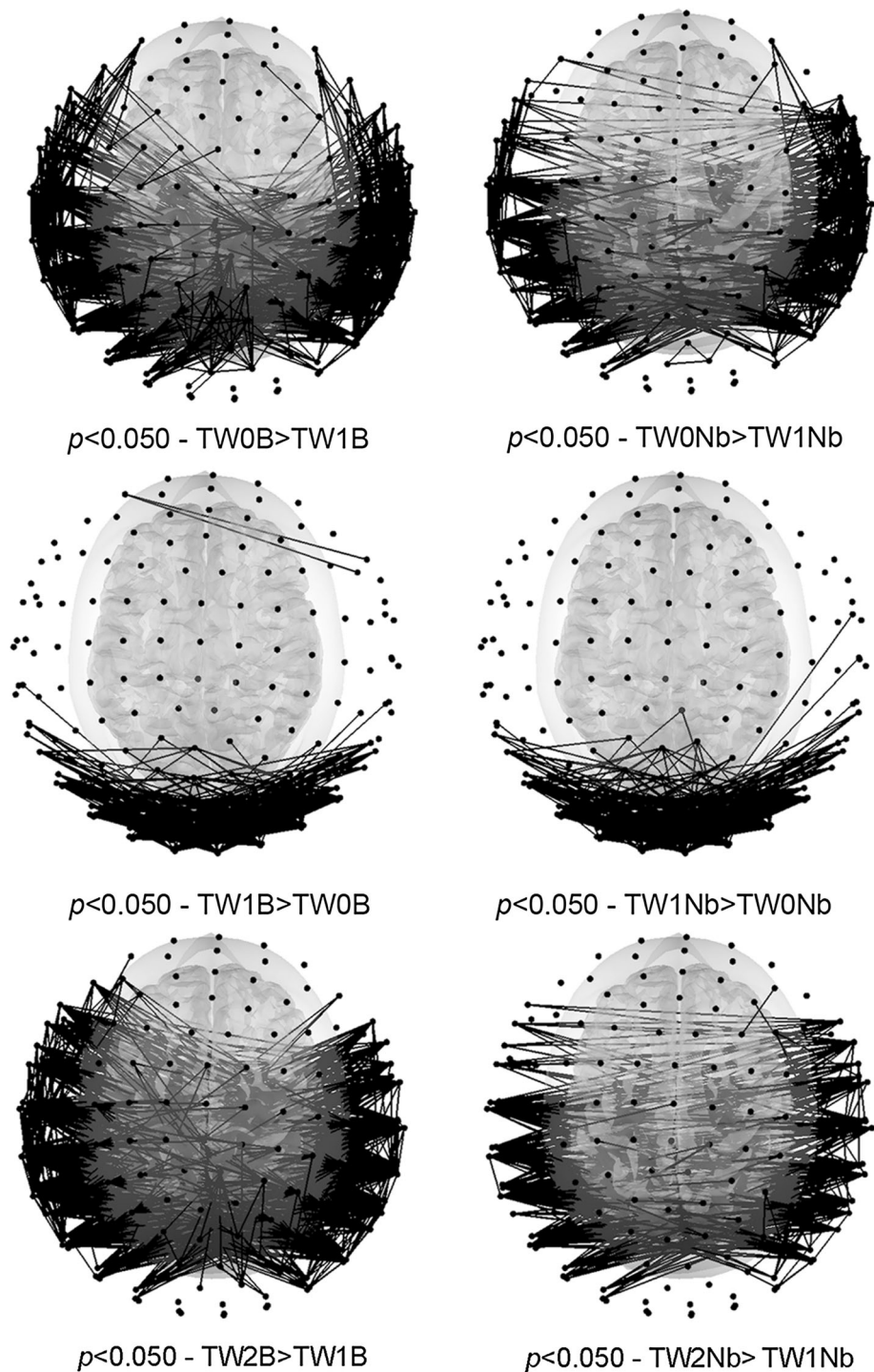


Fig. 2 Differences in synchronization before beautiful (*left*) and not-beautiful (*right*) stimuli. *Top* TW1 > TW0. *Bottom* TW2 > TW1



3 Aesthetics as an evolved 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 are distributed globally. Moreover, people are able to recognize products of other cultures as artworks. This general character is, in the opinion of Carroll (2004), an

argument in favor of considering that art may serve universal adaptive purposes. In other words, aesthetics could be an evolved human trait.

However, such hypothetical evolution 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

Table 3 Number of MEG sensors and links more synchronized in the inter-condition comparisons at $p < 0.050$

	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

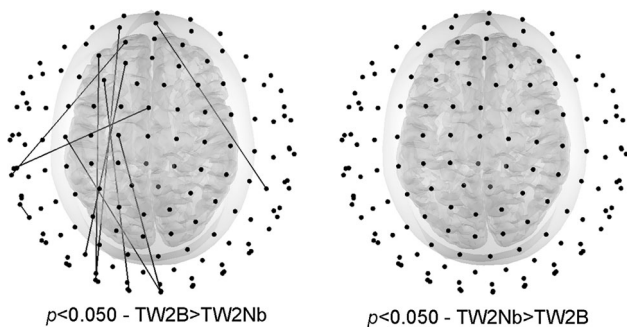


Fig. 3 Inter-condition comparison in the second temporal window (TW2). *Left* higher synchronization for beautiful stimuli. *Right* higher synchronization for not-beautiful stimuli

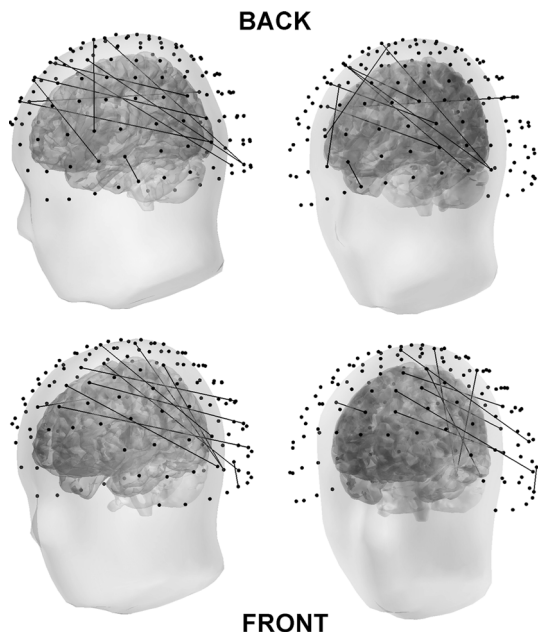


Fig. 4 The delayed aesthetic network from different perspectives

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) Thus, the adaptive advantages of the aesthetic appreciation need to be accounted for.

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?

The phylogenetic appearance of the brain correlates for appreciating beauty cannot at present be ascertained. Neither fossil, nor archaeological records provide enough evidence showing the evolution of such capacity. In spite of the existence of conspicuous artworks leading to the pinnacle of cave paintings, little is known about the evolution of the brain architecture, beyond general patterns on the Neanderthal vs. modern humans morphologies (Bruner and Holloway 2010; Bruner et al. 2003; Roseman et al. 2011). However, human features may be distinguished by means of comparative approaches with non-human 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 default mode network 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's return to the identification between the DMN and the aesthetic networks.

4 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) stated 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 and collaborators (Brown et al. 2011) held that "such a system evolved first for the appraisal of objects of survival advantage, such as food sources, and was later co-opted in humans for the experience of artworks for the satisfaction of social needs".

Obviously, any hypothesis in this field is difficult to test. However, a complementary justification for the evolution of capacities for appreciating beauty may be given by means of the coincidence between the delayed aesthetic network and the default mode network.

A fundamental function of the DMN is facilitating responses to stimuli. As Raichle and Snyder (2007) held that intrinsic brain activity "instantiates the maintenance of information for interpreting, responding to and even *predicting* environmental demands" (authors' emphasis). 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 default mode network 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, SIT onwards) (Mason et al. 2007). The SIT 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). SIT would enable subjects to maintain an optimal level of arousal. Alternatively, SIT would add coherence to one's experience—past, present. A non-adaptive meaning was also taken into account by these authors. SIT could be a byproduct 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 appreciation is not a stimulus-independent thought. Except in the case of recalling past experiences, detecting beauty depends on external stimuli. However, the aesthetic perception might be a byproduct 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. In the line of Kaplan (1987), the step forward from appreciating landscapes to re-create 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 electroencephalography (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).

5 Problems of the two-worlds issue

The internal, but stimulus-dependent visual appreciation of beauty is an individual instance of subjective and conscious experience—what philosophers call "qualia" (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.

Some aspects of the appreciation of beauty 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 quale, consisting of a description of brain 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 quale—the eventual result of beauty, or its absence, as an inner sensation—remains out of our reach.

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