Dynamics of brain networks in the aesthetic appreciation

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Neuroimage experiments have been essential for identifying active brain networks. During cognitive tasks as in, e.g., aesthetic appreciation, such networks include regions that belong to the default mode network (DMN). Theoretically, DMN activity should be interrupted during cognitive tasks demanding attention, as is the case for aesthetic appreciation. Analyzing the functional connectivity dynamics along three temporal windows and two conditions, beautiful and not beautiful stimuli, here we report experimental support for the hypothesis that aesthetic appreciation relies on the activation of two different networks, an initial aesthetic network and a delayed aesthetic network, engaged within distinct time frames. Activation of the DMN might correspond mainly to the delayed aesthetic network. We discuss adaptive and evolutionary explanations for the relationships existing between the DMN and aesthetic networks and offer unique inputs to debates on the mind/brain interaction.

Since the appearance of the first neuroimaging articles on aesthetics (1–3), a considerable number of studies have drawn a complex picture of the neural processes underlying people's aesthetic preference for visual and auditory stimuli. Many brain regions seem to be relevant for aesthetic appreciation. However, three sets of regions are often reported in the experimental results—those related to (*i*) reward/pleasure and emotion, (*ii*) judgment/decision making, and (*iii*) perception (*SI Methods* and Tables S1 and S2).

Most experiments have aimed at identifying brain regions whose activity varies with the aesthetic experience. Some studies, however, like Jacobsen et al. (4) and Vessel et al. (5), have reported brain activity in terms of putative networks, pointing to a network consisting of medial parts of frontal cortex (FMC), precuneus (PCUN), and posterior cingulate cortex (PCC), among other regions. These interconnected regions partly match the default mode network (DMN), corresponding to a baseline state of the human brain in awake but resting conditions (resting state) (6).

Brain Connectivity Related to DMN

The argument that a brain network exists lies in the assumption that some kind of connectivity exists between the areas involved. Following Von der Malsburg and Schneider (7), connectivity is associated with the presumable synchronization of neuronal assemblies—synchronous "firing." Distributed local networks of neurons would, eventually, be transiently linked by reciprocal dynamic connections (8).

"Functional connectivity" (9, 10) is defined as the statistically temporal dependency of neuronal activation patterns of anatomically separated brain regions (11). To uncover such dependency, temporal series of activation/deactivation of hypothetically synchronized brain regions must be compared. Such temporal series can be obtained, for instance, by detecting changes in blood oxygen content (blood oxygen level dependent signals) (12)—due to neural activity.

Raichle et al. (6), using positron emission tomography (PET), were able to identify the DMN, subsequently confirmed with functional magnetic resonance imaging (fMRI) (13). Several variables affect DMN activity, such as age, experience, and disease (6). Despite this variability, resting-state studies using different subjects, different methods, and different types of acquisition protocols have consistently reported that the DMN consists at least of the precuneus, medial frontal, inferior parietal, and medial temporal areas (11). The breadth of the DMN has been extended to include ventral anterior cingulate cortex, bilateral inferior parietal cortex, left inferolateral temporal cortex (14), and even the hippocampus (14, 15).

Although, as we will see later, some relationships between DMN and executive tasks—particularly involving working memory—exist, the activity of the DMN is curtailed when participants perform attention-demanding, goal-directed activities (6, 13, 16). Tasks asked by Jacobsen et al. (4) and Vessel et al. (5) of their participants required cognitive processes that rely on attentional resources. Consequently, the engagement of the DMN during aesthetic appreciation seems surprising.

Processes Related to Aesthetic Appreciation

In neuroaesthetic experiments, the tasks usually required from participants involve at least the processes of (*i*) viewing stimuli, (*ii*) appreciating their aesthetic qualities, (*iii*) rating their value, and (*iv*) formulating a response. These cognitive processes seem not to occur simultaneously. By means of electroencephalography (EEG), Jacobsen et al. reported that descriptive judgments of symmetry are performed faster than evaluative appreciation of their beauty (17). In turn, Locher et al., drawing from behavioral experiments and semantic judgments, interpreted that perception of art "begins with the rapid generation of a gist reaction followed by scrutiny of pictorial features" (ref. 18, p. 55). Similarly, Winkielman and Cacioppo (19) held that beautiful objects, at least, elicit positive emotions before subjects make overt judgments. In a different domain, Haidt proposed the existence in moral judgments of a quick, unconscious, and automatic evaluation (moral intuition), followed by a posterior reasoning process in which subjects search for justification of their intuitive judgment (moral reasoning) (20). Although Haidt's model is grounded in behavioral experiments, this is particularly interesting because several authors—including Jacobsen et al. (4)—have posited the eventual existence of brain mechanisms shared by aesthetic and moral judgments (21–24). Thus, coincidence between moral and aesthetic brain networks might occur.

Regarding aesthetic perception, the following null hypotheses can be expressed:

i) An initial, general appraisal of the aesthetic qualities, consisting of the perception of a visual stimulus as "beautiful" or "not beautiful," is performed very quickly. The neural correlates of such aesthetic appreciation constitute a network. We call this general process "aesthetic appreciation *sensu stricto*" and the network it relies on the "initial aesthetic network."

ii) Particular appraisals of detailed aspects of beauty, such as gauging the extent to which the stimulus is moving, whether it is interesting or original, how to rate it, the reasons for considering it attractive, and so forth, are performed later. We call these detailed processes "aesthetic appreciation *sensu lato.*" Putative networks formed by the neural correlates of such detailed aspects might be reduced to just one: the "delayed aesthetic network."

To which network would the DMN correspond: initial, delayed, both, or none? To give an answer, it is necessary to empirically determine the brain networks involved in aesthetic appreciation, as well as the time frame in which they are active. Once this has been clarified, the possible coincidence between the DMN and one or more aesthetic networks can be ascertained.

Experiment on Brain Connectivity During Aesthetic Appreciation

Our null hypotheses refer to cognitive processes taking place in a short timescale, compared with the relatively stable condition of subjects' brain activity during the resting state. Some studies have focused on the dynamic changes in brain networks, using fMRI (25), but, when the whole brain is considered, their time windows cover several seconds. Therefore, to test our hypotheses we are forced to use higher temporal-resolution techniques.

With a temporal resolution of milliseconds, magnetoencephalography (MEG), which detects changes in the magnetic fields generated by the postsynaptic activity of neurons, is one of such techniques. By means of MEG, we have obtained temporal series of brain activity for 24 participants during the resting state and during aesthetic appreciation of visual stimuli. Four hundred stimuli were successively projected and participants decided whether each stimulus was beautiful or not beautiful (*SI Methods*).

The MEG signals were split into three time windows and two evaluative conditions. Artifact-free time windows of 500 ms before stimuli projection were manually extracted for further connectivity analysis, constituting time window (TW0). After each stimulus onset, 1,500-ms artifact-free epochs were divided into two additional time windows: TW1, 250–750 ms; and TW2, 1,000–1,500 ms (Fig. 1, *Upper*). The length of the windows was determined by taking into account the time span in which brain activity can reach frontal areas during aesthetic appreciation (3). Before 250 ms, cognitive processes related to aesthetic appreciation rely mostly on visual-processing occipital areas (26). In

turn, MEG signals corresponding to the participants' stimuli appreciation were grouped, constituting the beautiful and not beautiful conditions.

Two different comparative strategies were carried out. Interwindows comparisons evaluated differences in connectivity between temporal windows along each condition (Fig. 1, *Lower Left*). Interconditions comparisons evaluated differences in connectivity between beautiful and not beautiful stimuli in each temporal window (Fig. 1, *Lower Right*). We estimated the synchronization of temporal series in the beta band by means of Pearson's correlation coefficient and phase locking value (PLV) (27, 28) (for a justification of the band selected see *SI Methods, Bands* section; the PLV algorithm is also described in *SI Methods*). In all cases, $P < 0.05$.

Results

Our analyses measure phase synchronization and amplitude correlation between time traces of activation of MEG sensors. In our case, connectivity is expressed by a bounded [0–1] weight, related to the amount of channel-wise synchronization. We infer functional connectivity from these measures. Thus, "connectivity" and "synchronization" can be taken here as equivalent concepts from the point of view of brain communication, despite the lack of information about the anatomical connectivity between neuronal regions and their precise localization. Although correlation takes into account the amplitude of a signal, phase synchronization can be observed even in the absence of amplitude synchronization (*SI Methods*).

Interwindows Analyses. Differences in synchronization appear in Table 1 (for complete results, see Table S3).
TW0 vs. TW1. Compared with TW1, TW0 shows more synchronized pairs of MEG sensors in both conditions (Table 1). The higher TW0 connectivity extends contralaterally from anterior occipital to anterior parietal, linking both hemispheres (Fig. 2, *Upper*).

In turn, TW1 > TW0 show similar numbers for both conditions (Table 1), with the higher TW1 connectivity placed in occipital regions (Fig. 2, *Lower*).
TW0 vs. TW2. Connectivity differences are fewer in TW0 > TW2 compared with the TW0 > TW1 case (Table 1 and Fig. S1, *Upper*). TW2 > TW0 does not show any difference (Table 1 and Fig. S1, *Lower*).
TW1 vs. TW2. TW1 > TW2 connectivity is more apparent in the not beautiful stimuli (Table 1). The higher TW1 synchronization appears in occipital–parietal links under both conditions. Moreover, in the not beautiful condition it extends from the occipital and parietal to the orbitofrontal region (Fig. 3, *Upper Right*).

TW2 > TW1 synchronization reveals the opposite trend: The number of links and sensors that are more activated is higher for the beautiful condition (Table 1). Also, the pattern of synchronization differs. TW2 > TW1 bilaterally reveals higher
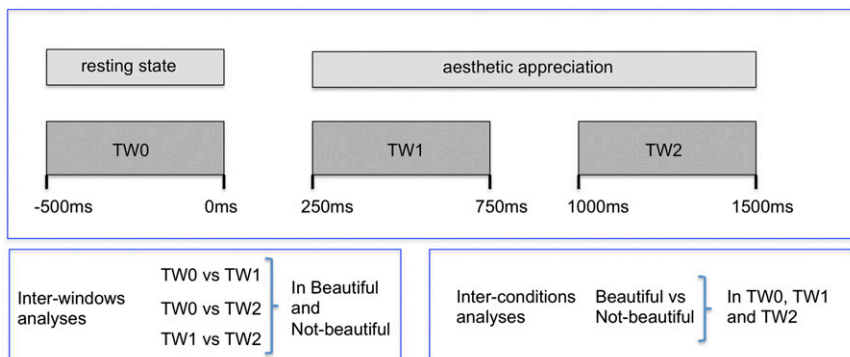

Fig. 1. Temporal windows, conditions, and comparative analyses used in our experiment.

Table 1. Number of sensors (*S*) and links (*L*) more synchronized in the interwindows comparisons at *P* < 0.05

Windows	Beautiful		Not beautiful	
	S	*L*	*S*	*L*
TW0 > TW1	117	1,012	98	695
TW1 > TW0	58	310	58	328
TW0 > TW2	13	8	23	15
TW2 > TW0	0	0	0	0
TW1 > TW2	51	282	63	389
TW2 > TW1	112	1,087	83	431

synchronization shared along parietal to temporal regions. In the beautiful condition, it is more medially and frontally placed. In the not beautiful condition, apart from being reduced, it is more laterally placed (Fig. 3, *Lower*).

Interconditions Analyses. Differences in synchronization appear in Table 2 (the complete results appear in Table S4).
TW0. Intercondition comparisons show minimal significant differences either in beautiful > not beautiful or in the opposite case (Table 2 and Fig. S2).
TW1. Also, intercondition comparisons show minimal significant differences either in beautiful > not beautiful or in the opposite case (Table 2 and Fig. S2).
TW2. In TW2, not beautiful > beautiful does not manifest differences either. On the contrary, beautiful > not beautiful analysis shows 19 sensors more connected (Table 2), with links extending from occipital and parietal to frontal regions in the left hemisphere (Fig. 4, *Lower*).

Discussion

If we compare interwindows and interconditions analyses, the most conspicuous difference appears in the number of sensors

p<0.050 - TW0B>TW1B   p<0.050 - TW0Nb>TW1Nb

p<0.050 - TW1B>TW0B   p<0.050 - TW1Nb>TW0Nb

Fig. 2. Differences of synchronization between TW0 and TW1. (*Left*) Under the beautiful condition (brain regions more connected before stimuli qualified as beautiful by participants). (*Right*) Under the not beautiful condition. (*Upper*) TW0 > TW1 synchronization. (*Lower*) TW1 > TW0 synchronization.

p<0.050 - TW1B>TW2B   p<0.050 - TW1Nb>TW2Nb

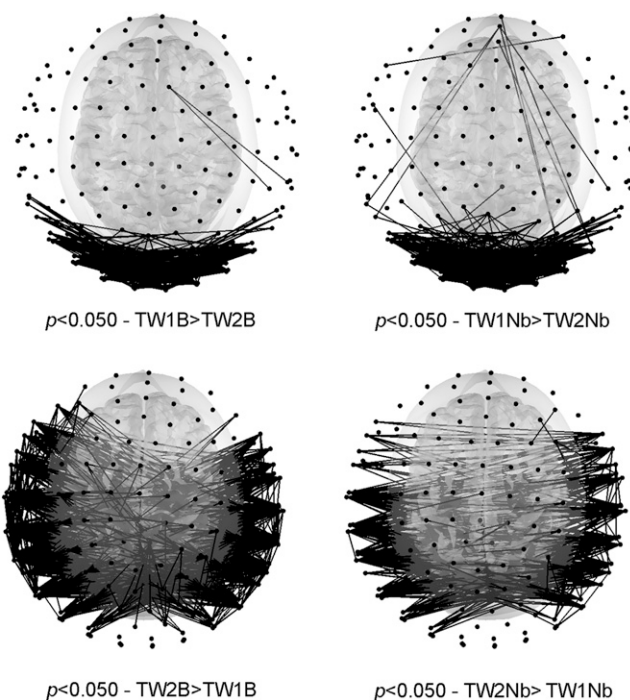p<0.050 - TW2B>TW1B   p<0.050 - TW2Nb> TW1Nb

Fig. 3. Synchronization in TW1 and TW2 under beautiful (*Left*) and not beautiful (*Right*) conditions.

and links implied (Tables 1 and 2 and Figs. 3 and 4). Interwindows differences affect extended networks in all cases, whereas interconditions differences are few. This is an expected outcome. Interwindows analyses refer to the dynamics of a cognitive process, that of appreciating beauty, which, as our hypotheses hold, may suffer considerable changes along the different time windows. This means that distinct brain networks will be activated in each case, leading to strong differences in connectivity. In turn, interconditions analyses refer, in the same time window, to the process of appreciation of beauty. Differences will appear only after reaching its result, beautiful or not beautiful, implying subtle changes in connectivity because most of the cognitive resources are the same when an object is considered beautiful or not beautiful.

Resting-State Issue. Both recent experience and consolidated abilities leave memory traces that affect the resting-state brain networks (15, 29). This is particularly important regarding the specific conditions of TW0, taken as the resting state of our experiment. Participants were quickly aware of the upcoming cognitive task to be performed, on the grounds of their recent experience. Moreover, they were soon habituated to the task of judging the beauty of stimuli. Thus, probably our participants had a TW0 network organization biased by the cognitive tasks to be developed.

However, our subjects could not anticipate the condition of the incoming picture. Thus, TW0 synchronization should be similar under beautiful and not beautiful stimuli. Interconditions analysis for TW0 indicates this coincident synchronization (Table 2). The few random differences that appear (Table 2) can be attributed to statistical fluctuations caused by the small number of sampled individuals.

Fig. 2, *Upper* shows in sagittal view how TW0 is more connected than TW1 mainly in occipital, temporal, and parietal areas. In turn, interwindows TW0 > TW1 analysis manifests a curtailing of the resting-state connectivity during TW1, affecting both conditions (Table 1). As is well known, the DMN fades when attentional tasks, such as seeing the projected stimuli, are performed. Our results support this curtailing in TW1.

Brain network differences present in the TW0 to TW1 dynamics disappear when TW0 is compared with TW2 (Table 1).
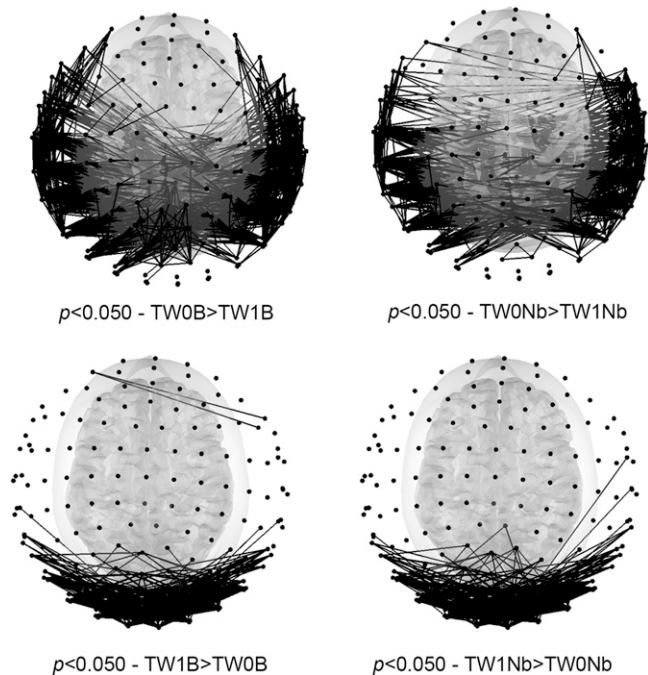
Table 2. Number of sensors and links more synchronized in the intercondition comparisons at $P < 0.05$

Windows	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

This result indicates that the brain networks active during the resting state and diminished in TW1 are somehow reestablished in TW2. We will come back to this point when discussing the delayed aesthetic network.

Twofold Model of Aesthetic Appreciation. TW1, compared with TW2, shows a different pattern of synchronization under beautiful and not beautiful conditions (Fig. 3). The results, thus, support our hypothesis about the existence of distinct cognitive events taking place at different time spans—what we call aesthetic appreciation *sensu stricto* and aesthetic appreciation *sensu lato* processes. Identification of such processes highlights the existence of a dynamical structure embedded within the whole episode of aesthetic appreciation. Also, a distinct network is related to each process—initial aesthetic network/aesthetic appreciation *sensu stricto* vs. delayed aesthetic network/aesthetic appreciation *sensu lato*. This twofold model of aesthetic appreciation is probably the main achievement of our work.

Initial Aesthetic Network. Comparisons between TW0 and TW1 reflect, under both conditions of beauty, that the brain connectivity present in the resting state is substituted during aesthetic appreciation *sensu stricto* by a network that mainly connects occipital regions: the initial aesthetic network. The task of identifying
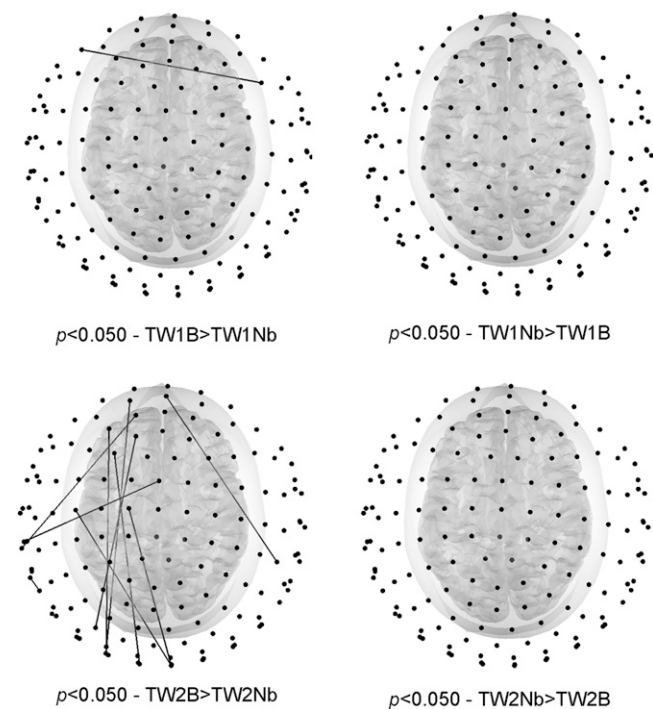

$p<0.050$ - TW1B>TW1Nb

$p<0.050$ - TW1Nb>TW1B

$p<0.050$ - TW2B>TW2Nb

$p<0.050$ - TW2Nb>TW2B

Fig. 4. Intercondition differences in synchronization at TW1 and TW2. (*Left*) Higher synchronization for the beautiful condition. (*Right*) Higher synchronization for the not beautiful condition.

cognitive processes related to these network dynamics is not easy. Compared with TW2, TW1 synchronization is higher in the not beautiful case (Table 1). It includes links extending from occipital to frontal regions, particularly the orbitofrontal cortex (OFC) (Fig. 3, *Upper Right*). The activation of OFC has been related to not beautiful stimuli appreciation (30), so the lack of frontal synchronization in the beautiful condition in the TW1 > TW2 comparison may suggest that beautiful stimuli do not activate OFC during TW1. However, this conclusion would lie in a misunderstanding. As we have already mentioned, our analyses are grounded in comparisons of connectivity, so equally synchronized regions do not yield differences. An OFC equally connected in TW1 and TW2 will not appear in the comparison between these windows. To check the eventually distinct degree of synchronization in OFC—or any other area—before beautiful vs. not beautiful stimuli we must use the interconditions analysis.

Interconditions analyses of synchronization during TW1 give almost no significant difference between beautiful and not-beautiful stimuli (Fig. 4, *Upper*). This means that, during TW1, all brain regions reached by our analysis—OFC among them—would be equally synchronized in both conditions. TW1 > TW2 connectivity in frontal regions for the not beautiful condition must, then, be grounded on a curtailing during TW2. We can state that the aesthetic appreciation *sensu stricto* (that one corresponding to TW1) implies common, shared cognitive processes regardless of the stimuli beauty or lack of it, giving OFC an important role in the initial aesthetic network.

The activation of OFC has been consistently related to reward and punishment (31–33). It processes information about the identity and reward value, associating visual stimuli to taste and touch primary reinforcers (34). However, our concerns refer to its linking paths. OFC, medial prefrontal, and the central nucleus of the amygdala form part of the central autonomic network, which controls appetitive (approach) and aversive (withdraw) behavior (35). Primate OFC receives information about the sight of objects from the temporal lobe cortical visual areas, contributing to stimulus-reinforcement association learning (34, 36–38). As Elliott et al. (39) stated, the OFC is likely to be activated when the problem of "what to do" before a visual stimulus is best solved by taking into account the likely reward value rather than its identity or location.

Emotional mechanisms related to OFC activation, such as those identified in many neuroaesthetics experiments, could also contribute to the increase of attentional resources, having an important role in decision making (31, 38, 40). Brown et al. (41) have pointed out that aesthetic pleasure is an object-related emotion, thus leading to pleasure and repulsion, whereas outcome-related emotion leads to happiness and disappointment. Visual stimuli, such as those normally used in neuroaesthetics, would be examples of "objects", whereas actions used in neuroethics—see Greene et al. (42), for instance—would constitute "outcomes". Appraisal of objects is strongly associated with OFC (40), something that is consistent with the idea that this region is "a form of higher-level sensory cortex receiving input from 'what' sensory pathways involved in object processing" (ref. 41, p. 251).

Assessment of beauty seems to appear in the dynamic transit from TW1 to TW2, because later latencies manifest—as we will immediately see—differences in synchronization depending on the putative previous results of beauty appreciation. The initial aesthetic network is visible during early latencies (250–750 ms). If this early process follows a parallel with Haidt's moral intuition, it would be performed automatically, in an unconscious manner, although easily accessible to consciousness.

Delayed Aesthetic Network. TW2 > TW1 connectivity is reflected by the pattern and number of sensors/links synchronized under the beautiful and not beautiful conditions, showing important differences between each case (Table 1). The scope and meaning of these differences are better understood by means of the interconditions analyses for TW2. Table 2 and Fig. 4, *Lower* show TW2 beautiful > not beautiful connectivity. The inverse

not beautiful > beautiful synchronization gives no result (Table 2). Moreover, it does not appear at any level of significance between $P < 0.01$ and $P < 0.1$ (Fig. S3). These results support our second hypothesis of existence of a delayed aesthetic network that is active only during the aesthetic appreciation *sensu lato* of beautiful stimuli. Fig. 5 shows the delayed aesthetic network under different perspectives.

The delayed aesthetic network consists of synchronized activity mainly present along left regions. Medial occipital, lateral occipital, lateral posterior parietal, medial parietal, medial frontal, and prefrontal in the left hemisphere are linked in it. It is important to underline that (*i*) we are focusing on MEG sensors connectivity, and (*ii*) just sensors more synchronized in the beautiful condition, compared with the not beautiful one, are identified.

Keeping in mind these limitations, relationships between the delayed aesthetic network and regions previously reported as active during the aesthetic appreciation can be stated. Many examples of activation in frontal, parietal, and occipital regions exist (Table S1). However, few studies on functional connectivity during aesthetic appreciation have been carried out, thus far. Brown et al. (ref. 41, p. 256) proposed a model of aesthetic processing consisting of "interaction between interoceptive and exteroceptive processing via recurrent connectivity between anterior insula and OFC," pointing out that this circuit "is in no way restricted to aesthetic processing, but may be related to all cognitive processes that involve viscerality [. . .] We propose that recurrent connectivity between the anterior insula and the OFC can mediate [. . .] the assignment of valence to objects." Thus, Brown et al.'s model would better correspond to the initial aesthetic network, where, incidentally, as we have seen, OFC has an important role. Similar patterns of functional connectivity along the reward circuit were offered by Tsukiura and Cabeza (22), Lacey et al. (43), and Faivre et al. (44). Lacking more accurate dynamic studies, all these works seem to cover aesthetic appreciation *sensu stricto* processes, in which resting-state synchronization is greatly diminished. What happens with the putative coincidence of the DMN with aesthetic networks?

DMN Role in Aesthetic Appreciation. As we have seen, the dynamic scenario during the aesthetic appreciation implies a late recovering, during TW2, of the TW0 brain synchronization. The DMN would thus coincide with some of the networks active during this late episode.

Under TW2 > TW1 comparison, beautiful and not beautiful conditions share a bilateral synchronization linking lateral regions along frontal–parietal–temporal–occipital areas (Fig. 3, *Lower*). In turn, the differences of synchronization in favor of beautiful stimuli seem to affect mainly medial parts of the brain. These differences are better shown in the TW2 intercondition analysis (Figs. 4, *Lower* and 5). On the basis of the combined interconditions and interwindows analyses, it seems that, despite the

moderate spatial accuracy of MEG signals at the sensors level, the delayed aesthetic network matches frontal, parietal, and temporal medial parts belonging to the DMN (Figs. 3 and 4). Moreover, this coincidence takes place only in TW2, and only under the beautiful condition. Fig. 6 shows in different perspectives more synchronized networks in TW2 vs. TW1 for each condition.

An intriguing question affects the recovering of part of the TW0 connectivity during TW2 when not beautiful stimuli are involved. As we have mentioned, in TW2 > TW1 comparison both conditions share a higher synchronization that is bilaterally expressed along temporal–parietal–occipital links (Fig. 3, *Lower*). This pattern matches the similar bilateral synchronization during TW0 (Fig. 2, *Upper*). These TW0 and TW2 highly connected regions, due to their lateral position, should have scarce relationship with the medially placed DMN.

According to He et al. (45), during the resting state the brain functional network consists not only of the DMN. Also, four other modules are active. Among them, module III mainly includes lateral parts of frontal and parietal regions, being involved in attention processing (45).

Two different networks related to attention have been indicated as relevant to guide conduct before stimuli of special importance. A dorsal frontoparietal network in the right hemisphere maintains endogenous signals based on expectation of seeing an object at a particular location, linking relevant stimuli to responses (46). A second system, the ventral frontoparietal network, responds along with the dorsal network when behaviorally relevant objects or targets are detected. This second network disappears when attention is focused, to prevent distraction, but is reactivated during reorienting events such as those needed by the unexpected appearance of objects (46). These kinds of tasks, also engaged in aesthetic appreciation, would be responsible for the activation of a putative reorienting network during TW2, shared by both beautiful and not beautiful conditions (Fig. 7). However, due to the lack of spatial accuracy of MEG at the sensor level, its coincidence with He et al.'s (45) module III is tentative.

Activation of the DMN has been proposed to occur during moral decision making (47–49), thus supporting the existence of brain mechanisms shared between moral and aesthetic appreciation *sensu stricto*. These common resources would strengthen the links between our hypotheses and Haidt's model of moral processes (20). Early episodes (moral judgment and aesthetic appreciation *sensu stricto*) do seem to have common features. However, the later moral reasoning, with its role as a self-justifying device, differs from our delayed aesthetic appreciation *sensu lato*. The latter seems to be quicker, not having any justificatory purpose. In actual fact, to decide to what point brain networks active during moral reasoning and aesthetic appreciation *sensu lato* are equivalent we would need to get both brain connectivity and its dynamics in moral judgment processes. Although some results on the presence of brain
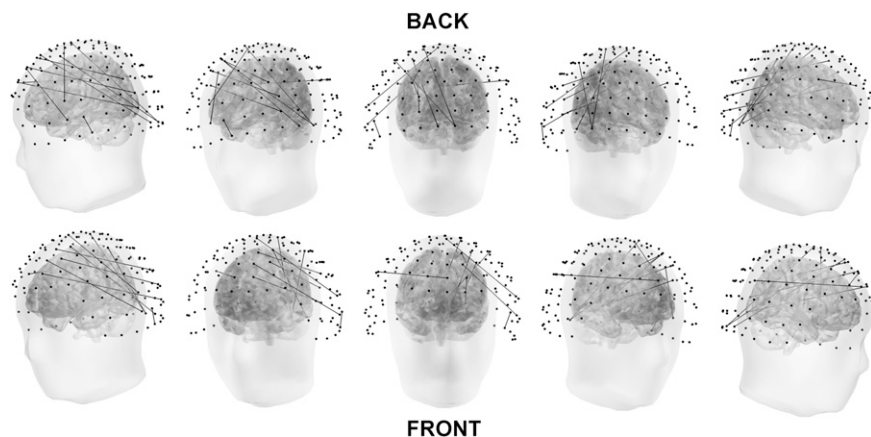
BACK

FRONT

Fig. 5. Delayed aesthetic network in the intercondition (TW2, beautiful > not beautiful) analysis.
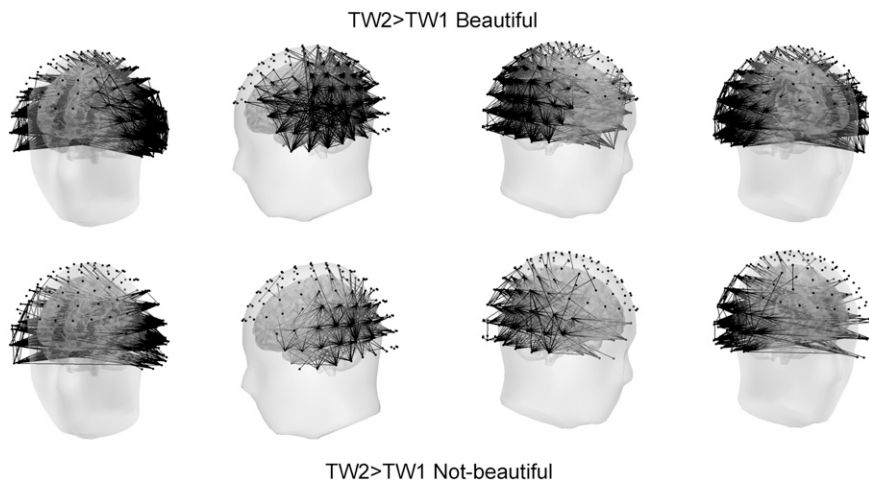
TW2>TW1 Beautiful

TW2>TW1 Not-beautiful

Fig. 6. TW2 > TW1 synchronization in beautiful (*Upper*) and not beautiful (*Lower*) conditions.

networks during moral reasoning exist (50), their dynamic analyses are currently lacking.

Adaptive Issues. It is well established that the brain is a metabolically expensive organ. In the awake resting state, the brain consumes 20% of the total oxygen in the body, despite that it represents only 2% of body weight (51). To explain evolutionary changes in the brain, costs/benefits ratios should be clarified (52). Thus, the adaptive advantages of any brain activity must be explained. What might the adaptive value of aesthetic appreciation be?

It has been held that aesthetics could be just an exaptation (53). Focusing on positive-valence aesthetic appraisals, Brown et al. (ref. 41, p. 257) argued that "[aesthetic processing] 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, this hypothesis is difficult to test—although it seems reasonably sound when trying to relate aesthetic appreciation to the adaptive advantages of emotions. However, the way in which this exaptation occurred still remains unexplained. The DMN–aesthetic appreciation link might help to justify it.

Raichle et al. (ref. 6, p. 681) posited that the function of the first region of the DMN, formed by the posterior cingulate cortex and adjacent precuneus, was to "continuously gather information about the world around, and possibly within us." Regarding the second region of the DMN, the medial prefrontal cortex would reflect "a dynamic interplay between ongoing cognitive processes and the emotional state of the subject [playing a role] in the integration of emotional and cognitive processes" (ref. 6, p. 682). Both functional capacities of the DMN seem adaptive enough to justify its metabolic costs. A different question is that of explaining how this link between the DMN and aesthetic appreciation appeared or, in other words, what characteristic of the DMN might lead to the sudden experiences of a picture's or a landscape's beauty.

An added function of the DMN relates it with "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 thought (SIT)] (54). This SIT is what we might call the mind talking with itself.

SIT could be a by-product of a general ability to manage concurrent mental tasks, acquired during human evolution (54). Nevertheless, Mason et al. (54) offered two possible explanations for the functional meaning of mind wandering. SIT would enable subjects to maintain an optimal level of arousal, as well as adding coherence to one's past and present experience.

DMN Activation During Executive Tasks. Remembering the past and imagining the future are processes that activate the DMN (55). In principle, mental simulations of the future are decoupled from achieving a particular goal, something that fits well with the fact that the DMN decreases its activity during attentional or executive tasks. However, when subjects are presented with imaginary scenarios in which they need to solve specific problems, some coactivity between the DMN and executive regions appears (56). It
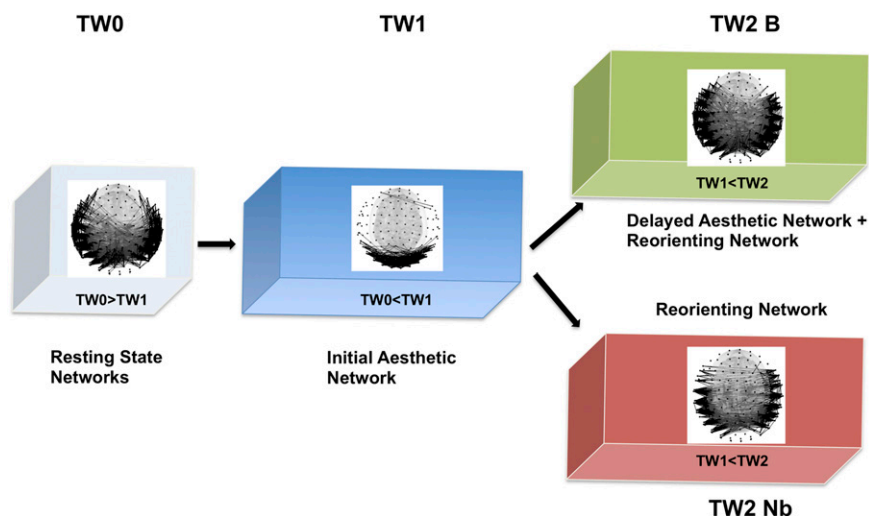
Fig. 7. Dynamics in the appreciation of beauty. TW0 networks (illustrated by the TW0 > TW1 comparison) fade during TW1, being substituted by a similar network shared by beautiful and not beautiful conditions (illustrated by the TW1 > TW0 comparison under the beautiful condition). During TW2, not beautiful stimuli activate a bilateral reorienting network, whereas beautiful stimuli add the delayed aesthetic network, more medially placed (in each condition, TW2 networks are illustrated by TW2 > TW1 comparison).

seems that simulating how to solve a problem in the future allows "task-positive network regions to be coactive with default network regions without suppressing the contribution of either network" (ref. 56, p. 1823). To do so, the DMN seems to cover two seemingly contrasting functions: spontaneous cognition and monitoring the environment. They need not be mutually exclusive, because they "represent complementary instances of conscious experiences occurring during idle moments of daily life" (ref. 57, p. 76). There is a growing body of evidence showing the complex relationships existing between inner thought and the processing of external events. It shows that traditional dichotomies, such as on task vs. off task, goal-free vs. goal directed, or mind wandering vs. mental target are inadequate to describe some processes of thought.

This seems to be the case of aesthetic appreciation.

Aesthetic appreciation is not an example of stimulus-independent thinking. Except when recalling past experiences or imaging objects or places, detecting beauty depends on external stimuli. However, aesthetic appreciation might be a by-product of the capacity for mind wandering. Mind wandering is a general, extended process of perception neither guided by any goal nor directed to any particular aspect. A close-to-mind-wandering capacity for assigning beauty or ugliness to visual stimuli could thus lead to continuous and fast processes of aesthetic appreciation. The combination of EEG and fMRI (58) allows us to relate the sudden comprehension that accompanies solving a problem or a perceptual ambiguity—known as the "Aha! moment"—with the culmination of a series of cognitive events starting at the resting sate. Regarding aesthetic appreciation, our current study suggests that the appreciation of beauty might also be an Aha! moment, the sudden result of a complex process to which the DMN and other networks contribute.

Aesthetic appreciation processes can be reached even if no previous purpose to evaluate beauty exists. The human capacity for aesthetic appreciation could be tentatively described as something like seeing the world continuously, in a not-oriented way, with an unconscious capacity for perceiving beauty that can almost instantaneously become conscious, constituting an Aha! moment. Everyday life perception of images and the ability to contemplate objects as likely to be seen as beautiful are different orientations that can lead to distinct cognitive processes (59). Nevertheless, we can posit that the Aha! moment also appears under experimental conditions when stimuli to be judged in aesthetic terms are expected to be seen. Natural and experimental conditions refer to processes that must rest on the same phylogenetically fixed cognitive mechanisms of appreciation of beauty, which include cooperation of the DMN with other perceptual, decisional, and emotional networks. On the grounds of our results, the Aha! moment would have a place when the results of aesthetic appreciation *sensu stricto* become conscious. If the DMN helps in this achievement, the Aha! moment might constitute an early episode during aesthetic appreciation *sensu lato*, i.e., in TW2. The first consideration that subjects perform, at the beginning of TW2, could be the awareness of the actual beauty or ugliness of stimuli.

The eventual relationship of this aesthetic Aha! moment with other episodes, such as that of problem solving, cannot be determined thus far. The cognitive processes related to problem solving and beauty appreciation seem very different from each other. Therefore, different brain networks might be implied. Nevertheless, once again, we need further studies of other Aha! synchronization dynamics to be able to check their eventual coincidence against the aesthetic networks identified by us.

Pathologic Alterations. Aesthetic appreciation compound complexity is supported by pathologic alterations of cognition. The DMN decreases its resting-state activity in patients with Alzheimer's disease (14, 60, 61). Crucial components of the DMN are damaged, impairing cognitive tasks related with explicit memory. Despite this, patients with Alzheimer's disease are still able to enjoy the aesthetic qualities of objects and express their aesthetic preference in a consistent manner, indicated by

highly similar ordering at different moments in time of representational, quasi-representational, and abstract picture cards, according to their preference (62). Halpern et al.'s (62) results show that patients with Alzheimer's disease are well aware of their personal, intrinsic appreciation of beauty and that they are also able to communicate its content. This fact implies that such patients (*i*) appreciate beauty in pictures, (*ii*) can compare pictures according to their beauty, and (*iii*) can order them consequently. The process affects not only aesthetic appreciation *sensu stricto*. Ranking the beauty of each stimulus, comparing them all, rating them, and reporting their response form part of aesthetic appreciation *sensu lato* and are realized in a stable manner over time. The capacity for appreciating beauty despite the impairment of DMN components supports the idea that aesthetic appreciation is achieved by means of a quite general coactivity of distinct networks across the brain. Although patients with Alzheimer's disease would probably have an altered experience of beauty, they keep enough cognitive resources to reach the aesthetic appreciation even in advanced stages of the illness (63).

Comparative Synthesis. Combining the previous results obtained with our current MEG results, the following panorama appears:

i) A fast aesthetic appreciative perception (aesthetic appreciation *sensu stricto*) is formed within the 250- to 750-ms time window (TW1), activating the initial aesthetic network.

ii) Further cognitive processes—aesthetic appreciation *sensu lato*—are subsequently performed within the 1,000- to 1,500-ms time window (TW2), relying on the delayed aesthetic network.

iii) The initial aesthetic network is involved in both conditions (beautiful and not beautiful), OFC having an important role in it.

iv) The delayed aesthetic network is composed of more synchronized links in the beautiful condition. It can be posited that matching with the DMN occurs only then, during the aesthetic appreciation *sensu lato*.

v) Initial and delayed aesthetic networks appear to be clearly separated in our analysis. However, this might be a result of the time-windows distribution. Because we have considered TW0, TW1, and TW2 to be separated by 250-ms time spans, an eventual gradual transition from the aesthetic appreciation *sensu stricto* to the aesthetic appreciation *sensu lato* would be hidden by the lack of information corresponding to the temporal borders. To decide the gradual or abrupt character of the transition, precisely identifying the Aha! moment event, more accurate analyses should be carried out.

Hard Problem. The internal but stimulus-dependent visual appreciation of beauty is a subjective experience, what philosophers call a "*quale*." How far have we come in understanding how the brain produces this mental result?

The soft problem of the mind/brain issue (64), consisting in our case of the localization of brain areas active when subjects gauge the beauty of a visual object, has already been clarified many times under different tasks and experimental conditions.

Combining results of fMRI, MEG, and behavioral studies, we seem to have begun scratching the surface of the hard problem (65), i.e., the way in which the experience of beauty could dynamically arise from the actions of the brain. This point has been only partly solved, thus far. It seems that the structure of the *quale*, consisting of a description of mental processes, can be accessed by means of scientific procedures regarding brain connectivity and its flow along time. Hopefully, we have offered some genuine inputs into the dynamics of aesthetic appreciation. However, for the time being, the content of the *quale*—i.e., the eventual result of beauty, or its absence, as an inner sensation

—is still out of our reach. Many personal circumstances, from previous experiences to character traits, plus health, age, and maybe sex, as well as cultural and historical particularities of each subject and epoch, surely contribute to the Aha! experience of appreciating beauty.

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Supporting Information

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SI Methods

Details of stimuli, experimental protocol, and methods of magnetoencephalography (MEG) acquisition and processing have been given elsewhere (1).

Stimuli and Participants. The stimuli consisted of artistic and natural colored pictures divided into five groups: (*i*) 40 pictures of abstract art; (*ii*) 40 pictures of classic art; (*iii*) 40 pictures of impressionist art; (*iv*) 40 pictures of postimpressionist art; and (*v*) 160 photographs of landscapes, artifacts, urban scenes, and so forth (true-life pictures from the Master Clips Premium Image Collection, IMSI; postcards; and photographs taken by us). We used, as a guide, styles selected from the collection *Movements in Modern Art* of the Tate Gallery, London, adding European XVII and XVIII Centuries and American Popular Art pictures. The Museo Nacional del Prado (Madrid) kindly gave us permission to use their artworks and reproduce them. The objective was to present subjects a variety of artistic styles to increase their choice of aesthetic judgment. To avoid the activation of facial recognition brain mechanisms, pictures containing close views of humans were discarded. All stimuli were adjusted to the same resolution (150 pixels per inch) and dimensions (12 × 9 cm). Details of the adjustment to homogeneous conditions can be found in Cela-Conde et al. (2).

Twelve female and 12 male neurobiology students (average age 23.6 y for women and 25.1 y for men) at the Universidad Complutense (Madrid), with no previous training or special interest in art, volunteered to participate in this study. They all had normal or corrected vision and normal color vision. All were right-handed. All participants gave informed consent.

Conditions. *Task-free.* MEG data before stimuli projection were recorded while participants lay comfortably, eyes open, in a quiet and low-illuminated room, with no tasks given.

Aesthetic judgment. MEG data corresponding to aesthetic judgment were recorded while participants viewed 400 images of unfamiliar paintings by artists from different artistic movements and styles and photographs depicting diverse objects and landscapes, urban and rural. Participants were asked to indicate whether they found each image beautiful or not, emphasizing the importance of expressing their own impressions. The results of appreciation were given by pressing a button [answer counterbalanced for beautiful (B) and not beautiful (Not-b) decisions].

Data Analysis. *MEG data acquisition.* During the aesthetic appreciation task, the MEG signal was recorded while subjects lay on a horizontal stretcher. Images were projected through a liquid crystal display (LCD) video projector, situated outside of the shielded room, onto a series of in-room mirrors, the last of which was suspended ∼1 m above the participant's face. A sampling rate of 678 Hz and a band-pass filter between 1 Hz and 48 Hz were applied, using a 148-channel whole head magnetometer (MAGNES 2500WH; 4D Neuroimaging) confined inside a magnetically shielded room.

For further off-line processing, visual inspection of the MEG signals through MATLAB 2011b software allowed the selection of a minimum of 36 artifact-free epochs for each subject by a trained investigator. Given the narrowness of the time windows considered in this work, a sixth-order second-order sections (SOS) filter was able to extract the beta frequency band (15–25 Hz) with minimum border effect.

Bands. Typical brain signals have broad bands; however, their analysis might yield wrong conclusions (3) due to, at least, two reasons. Slow-frequency bands contain few cycles in the short time windows we considered (500 ms), leading to an incorrect calculation of characteristic indexes. Fast frequencies are more susceptible to noise, because the signal-to-noise ratio diminishes. Previous studies have identified specific bands, such as the beta band, as those carrying more power during synchronization related to visual tasks in monkeys (4) and humans (5), as well as in aesthetic appreciation (6).

Nonlinear connectivity analysis. Functional connectivity is a suitable tool for the study of brain functioning (7). It provides information about interactions between brain regions through statistical interdependencies between two physiological signals. Computation of such interactions between all pairwise combinations of the 148 MEG channels was performed with the help of a new Matlab toolbox: HERMES (see Hermes: open source toolbox for time series connectivity analysis; http://hermes.ctb.upm.es). Verified implementations of phase locking value (PLV) and Pearson's correlation measures were applied. PLV (8) and Pearson's correlation coefficient were calculated in the following way.

PLV and correlation description. PLV is defined as

$$\text{PLV} = \left| \left\langle e^{i\Delta\phi_{rel}(t)} \right\rangle \right| = \left| \frac{1}{N} \sum_{n=1}^{N} e^{i\Delta\phi_{rel}(t_n)} \right| = \sqrt{\left\langle \cos \Delta\phi_{rel}(t) \right\rangle^2 + \left\langle \sin \Delta\phi_{rel}(t) \right\rangle^2},$$

where $\langle . \rangle$ indicates time average. $\Delta\phi_{rel} = \phi_x - \phi_y$, where ϕ is the phase calculated from the Hilbert transform of x and y signals.

The PLV estimates how the relative phase $\Delta\phi_{rel}$ is distributed over the unit circle (8, 9). When there is strong phase synchronization between the two time series, the relative phase is almost locked and the PLV is close to 1. If the signals are not synchronized, the relative phase would, on average, spread out all over the unit circle and the PLV would remain low (close to 0). Then, the range of the PLV is $0 \leq \text{PLV} \leq 1$.

Statistical Analysis. To perform the statistical analysis we need to compute the degree of phase synchronization and cross correlation between pairs of sensors for each participant, at time windows TW0, TW1, and TW2 and conditions B and Not-b. For example, w_{ij}^{B} would represent the weight (either PLV or the maximum of the cross-correlation function computed in a certain time window) of the link between sensors i and j computed for the beautiful condition averaged over the number of samples ranked as beautiful by the person that is analyzed. With these weights w_{ij}^{B} we compute the probability distribution function using data from the 24 people for the B condition in a given time window.

Nonparametric permutation testing, based on the Kruskal–Wallis test, was applied to find channel pairs with significant differences in the corresponding distribution functions between groups (10). This was done by randomly dividing the participants into two sets, matching the numbers in the original groups. The two-sample Kruskal–Wallis test was then carried out between these two new groups and for each channel pair. This was repeated 1,000 times and the P value from each test for each channel pair was retained to obtain a P-value distribution for each channel pair. We then identified the second percentile of each distribution, and only P values below that threshold ($P < 0.05$) were accepted.

Network Analysis. The statistical analysis provides us with a set of channel pairs of sensors whose synchronization level measured

either with PLV or with Pearson's correlation is significantly different, taking into account subject variability between time windows or between conditions (B and Not-b). In the comparisons, such as TW0 > TW1 in Fig. 2, networks were built, connecting these significantly different pairs of sensors by links with the extra condition that the median synchronization between those two sensors in TW0 is larger than in TW1. Each of the networks was thus characterized by a particular pattern of connectivity, with certain sensors without any link whereas others are highly interconnected. The number of sensors with connections is included in Table S3, as well as the number of links for the different time-window comparisons.

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p<0.050 - TW0B>TW2B   p<0.050 - TW0Nb>TW2Nb

p<0.050 - TW2B>TW0B   p<0.050 - TW2Nb>TW0Nb

Fig. S1. Differences in synchronization between TW0 and TW2 temporal windows in beautiful (B) and not beautiful (Nb) conditions.
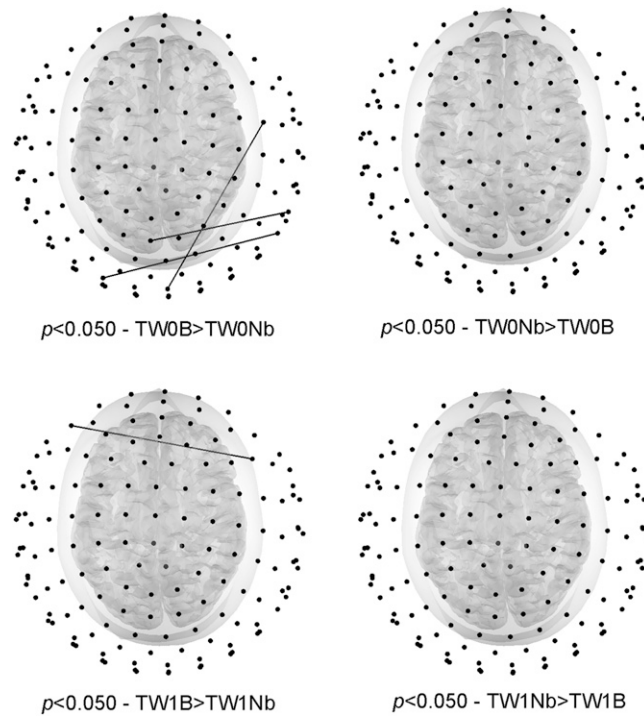
Fig. S2. Differences in synchronization between beautiful (B) and not beautiful (Nb) conditions in TW0 and TW1 temporal windows.
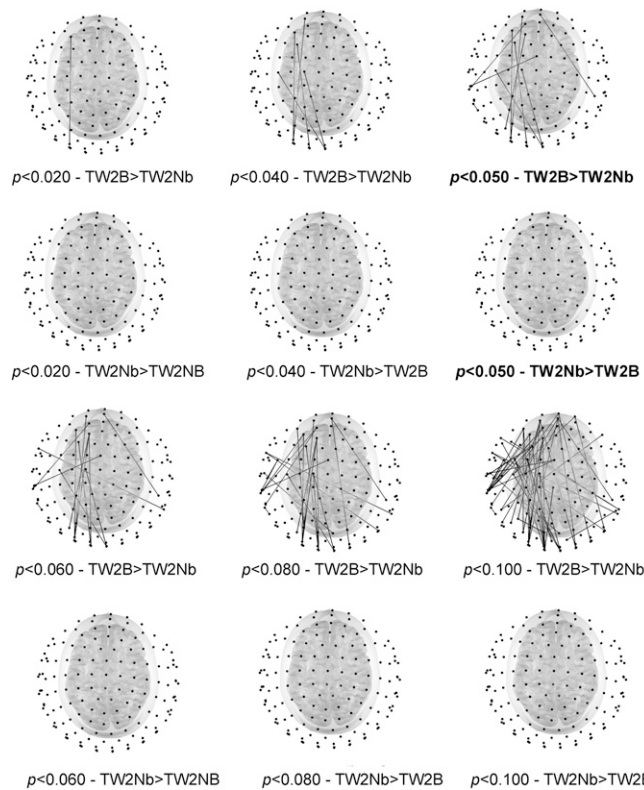

Fig. S3. Differences in synchronization between beautiful (B) and not beautiful (Nb) conditions in the TW2 temporal window at different levels of significance. In boldface type, $P < 0.050$.

Table S1. Active brain areas related to the aesthetic experience identified in 20 neuroaesthetics experiments (1–20)

Area	No.*	Cognitive processes
vMPFC: ventromedial prefrontal cortex	1	Default mode network
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 number of experiments mentioning each brain area.

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Table S2. Brain regions whose activity is related to aesthetic preference and corresponding Brodmann areas and Talairach coordinates

Area	Abbreviation	Brodmann area	Talairach coordinates			Ref. 1	Ref. 2
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	lTP	38	−43	2	−29	x	
Right tempoparietal junction	rTPJ	39/40/42	46	−56	32	x	
Left tempoparietal 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

Last two columns are according to Yang et al. (1) and Vessel et al. (2).

1. Yang F, Bao ZY, Zhu ZJ (2011) An assessment of psychological noise reduction by landscape plants. *Int J Environ Res Public Health* 8(4):1032–1048.
2. Vessel EA, Starr GG, Rubin N (2012) The brain on art: Intense aesthetic experience activates the default mode network. *Front Hum Neurosci* 6:66.

Table S3. Number of sensors (*S*) and links (*L*) more synchronized in the interwindows comparisons at $P < 0.05$

	Beautiful		Not beautiful	
Windows	S	L	S	L
PLV				
TW0 > TW1	117	1,012	98	695
TW1 > TW0	58	310	58	328
TW0 > TW2	13	8	23	15
TW2 > TW0	0	0	0	0
TW1 > TW2	51	282	63	389
TW2 > TW1	112	1,087	83	431
Correlation				
TW0 > TW1	119	1,016	99	702
TW1 > TW0	58	319	60	328
TW0 > TW2	11	7	24	16
TW2 > TW0	0	0	0	0
TW1 > TW2	51	258	62	380
TW2 > TW1	111	1,100	84	429

Table S4. Number of sensors and links more synchronized in the intercondition comparisons at $P < 0.05$

	PLV			
	Beautiful > Not beautiful		Not beautiful > Beautiful	
Windows	Sensors	Links	Sensors	Links
PLV				
TW0	6	3	0	0
TW1	2	1	0	0
TW2	19	10	0	0
Correlation				
TW0	6	3	0	0
TW1	2	1	0	0
TW2	17	9	0	0