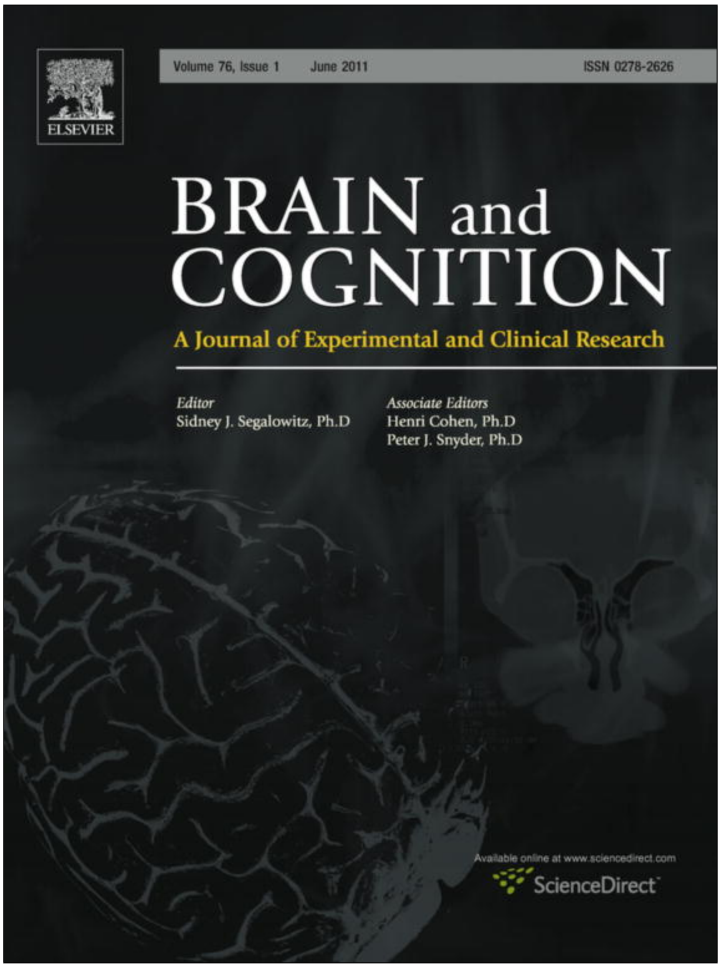
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The Copenhagen Neuroaesthetics conference: Prospects and pitfalls for an emerging field

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ABSTRACT

Neuroaesthetics is a young field of research concerned primarily with the neural basis of cognitive and affective processes engaged when an individual takes an aesthetic or artistic approach towards a work of art, a non-artistic object or a natural phenomenon. In September 2009, the *Copenhagen Neuroaesthetics Conference* brought together leading researchers in the field to present and discuss current advances. We summarize some of the principal themes of the conference, placing neuroaesthetics in a historical context and discussing its scope and relation to other disciplines. We also identify what we believe to be the key outstanding questions, the main pitfalls and challenges faced by the field, and some promising avenues for future research.

1. Introduction

Neuroaesthetics is still an emerging field of research. Although it draws on research in many disciplines, it is rapidly taking shape as a field of study in its own right with increasing numbers of journal articles and books contributing to its central themes. Some of the researchers at the field's forefront recently came together at the *Copenhagen Neuroaesthetics Conference* (24–26 September 2009) to present their latest research on the relations between artistic, philosophical, psychological, neural and evolutionary aspects of human aesthetic experiences. The conference also provided a forum for discussion and reflection on some of the field's core themes and problems. We start by examining the historical roots of neuroaesthetics and identifying its scope before reporting some of the contributions presented at the conference and framing them within the context of the existing neurobiological literature on the perception and production of visual art, dance and music. Space will preclude us from referring to all the talks and posters presented at the conference. So, throughout this paper we highlight only to those explicitly attempting to characterize the neural foundations of aesthetic experience and their evolution. We close by highlighting what we believe are the main challenges faced by this new field and the key research directions for its future development.

2. Historical roots of neuroaesthetics

The history of neuroaesthetics reflects the development and confluence of research in psychology, neuroscience, evolutionary biology and philosophical aesthetics. Historically, these disciplines have converged to examine aesthetic experience at the mid-eighteenth century, the late nineteenth century, and the late twentieth century.

Current thinking on the biological basis of artistic and aesthetic creation and appreciation has its roots in the works of British empiricists (Moore, 2002; Skov & Vartanian, 2009a). Drawing upon the Cartesian notions of the human body as a machine and animal spirits acting through the nerves to produce movements and convey sensory information, Edmund Burke (1757) elaborated a physiological explanation for the aesthetic experiences of sublimity and beauty. He argued that the former is supported by the same biological mechanisms as pain, while the physical causes of love and pleasure underpin the latter. Any stimulus capable of producing similar effects to the "unnatural tension, contraction or violent emotion of the nerves" (Burke, 1757, p. 248) that characterize pain, would lead to states of fear or terror, and would consequently constitute a source of the sublime. Conversely, "a beautiful object presented to the sense, by causing a relaxation in the body, produces

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the passion of love in the mind" (Burke, 1757, p. 287). These physiological explanations for aesthetic experiences were adopted and expanded by contemporary authors, such as Uvedale Price (1810) and Daniel Webb (1769, reproduced in Katz & HaCohen, 2003). Burke, Price and Webb's work reveals that neuroaesthetic themes emerged naturally as soon as a plausible physiological framework and adequate psychological concepts became available. However, as noted by Moore (2002), the widespread and lasting influence of Kant's (1790/1892) transcendental perspective separated aesthetic experiences from emotion and sensory pleasure, and brought to a halt this first physiological foray into aesthetics.

Work on the biological basis of aesthetic behavior did not emerge again until the second half of the 19th century, when Darwin (1859/1991) introduced the mechanism of natural selection to explain the evolution of organisms, and highlighted the role of sexual selection throughout human evolution (Darwin, 1871/1998). Some of the pioneering studies of early neuroscience were also carried out at this time, including the identification of the cortical mechanisms underlying language production and comprehension (Broca, 1863; Wernicke, 1874), and Brodmann's (1909) description of cortical cytoarchitectonic features. At the same time, the foundations of scientific experimental psychology were being established through the work of Fechner (1860) and Wundt (1873, 1874).

It was in this context of the flourishing fields of evolution, neuroscience and psychology that interest in the biological basis of aesthetics reappeared. Strongly influenced by Darwin's natural selection, Clay (1908) argued that humans' aesthetic appreciation conferred on mankind the selective advantage of being able to assess the suitability of the environment around us in terms of its resources and potential dangers. The role of sexual selection in the origin and evolution of aesthetic appreciation was emphasized by Allen (1880) and Darwin (1871/1998) himself. Habitat selection and mate choice remain today two of the strongest explanations of the origin and evolution of our capacity to appreciate beauty (Dissanayake, 2007). The work of Marshall (1894), who developed the 18th century notion that aesthetic experiences are mediated by the neural mechanisms of pleasure and pain, and updated it with the neurophysiology of the time, constitutes an excellent example of late 19th century neuroaesthetics.

In retrospect, it might seem that the period between the mid nineteenth and early twentieth centuries had set the stage for a golden age of neuroaesthetics. However, this turned out not to be, as further developments of the field were frustrated by the advance and subsequent dominance of behaviorist psychology championed by Thorndike (1911), Watson (1913) and Skinner (1938). Even Fechner's (1876) empirical aesthetics was unable to develop and strengthen its links with the neurosciences in one direction and evolutionary theory in the other. In Colin Martindale's words, the behaviorist era was "an unmitigated disaster for psychological aesthetics" (Martindale, 2007, p. 123). The reduction of psychology to the study of overt behavior deprived neuroscientists and evolutionary theorists of a detailed account of cognitive and affective processes involved in aesthetic experiences. Hence, in spite of amazing advances made in evolutionary biology and neuroscience during the first half of the 20th century, there was no psychological framework that could integrate such developments into a comprehensive picture of the evolutionary and neural foundations of aesthetic creation and appreciation.

However, neuroscientists and evolutionary theorists saw no reason to wait for psychologists to regain interest in cognition generally, and aesthetics in particular. Neurologists examined the relation between brain injuries, often associated with aphasia, and artistic or aesthetic activities (Alajouanine, 1948; Gourevitch, 1967; Luria, Tsvetkova, & Futer, 1965; Zaimov, Kitov, & Kolev, 1969) and no sooner had evolutionary biologists turned to human behavior than they began to write on aesthetics (Alland, 1977; Eibl-Eibesfeldt, 1988, 1989; Wilson, 1975).

Eventually, the tradition of empirical aesthetics founded by Fechner (1876) was given new life by the research of Daniel Berlyne (1971, 1974). As a result, the psychological approach to aesthetic and artistic appreciation and creation gained momentum during the last few decades of the twentieth century. The dialogue between psychology and neuroscience was complemented by several theoretical proposals hypothesizing links between specific brain activity and certain aspects of aesthetic experience based on the growing knowledge of brain function (Changeux, 1994; Miall, 1977; Ramachandran & Hirstein, 1999; Zeki, 1998, 2001; Zeki & Lamb, 1994).

We believe that two fundamental developments afforded researchers a third chance to consolidate the field of neuroaesthetics around the turn of the millennium. First, the notion of a single special mechanism underlying aesthetic experiences has been dropped in favor of the view that aesthetic appreciation and related phenomena rely on several general mechanisms, including processes of perception, memory, attention, decision-making, and reward and emotion (Chatterjee, 2004a; Leder, Belke, Oeberst, & Augustin, 2004). Given what we know of the neural correlates of such processes, it follows that aesthetic experiences must emerge from the dynamic interaction of activity in multiple brain regions at different time frames.

The second shift is methodological in nature. Until recently only two strategies were available for studying the biological mechanisms underlying artistic appreciation and creation: first, making theoretical conjectures based on general understanding of brain structure and function; and second, single case-studies of brain injuries affecting art-related activities. The former produced theories that often went untested (and were sometimes untestable), while the latter generated accounts that were often anecdotal, incomplete and difficult to interpret. However, the advent and refinement of non-invasive neuroimaging techniques has permitted the empirical study of healthy participants' aesthetic experiences in controlled situations, affording the opportunity to draw general conclusions about the neural processes underlying the perception and production of art (Brattico & Jacobsen, 2009; Cela-Conde et al., 2009; Cupchik, Vartanian, Crawley, & Mikulis, 2009; de Tommaso et al., 2008; Di Dio, Macaluso, & Rizzolatti, 2007; Fairhall & Ishai, 2008; Ishai, Fairhall, & Pepperell, 2007; Kirk, Skov, Christensen, & Nygaard, 2009; Kirk, Skov, Hulme, Christensen, & Zeki, 2009; Koelsch, Fritz, von Cramon, Müller, & Friederici, 2006; Lengger, Fischmeister, Leder, & Bauer, 2007; Müller, Höfel, Brattico, & Jacobsen, 2009; Yue, Vessel, & Biederman, 2007).

3. The Copenhagen Neuroaesthetics Conference: A timely event

Six years have now passed since the first applications of neuroimaging to aesthetic appreciation of paintings (Cela-Conde et al., 2004; Jacobsen, Schubotz, Höfel, & von Cramon, 2006; Kawabata & Zeki, 2004; Vartanian & Goel, 2004) and the first thorough reviews of the effects of brain lesions on artistic production and appreciation (Chatterjee, 2004b, 2006; Zaidel, 2005). Subsequently, the number of neuroimaging studies has exploded, as the sample of citations in the preceding paragraph shows. Although all these studies share the common goal of understanding the neural underpinnings of aesthetic behavior, there are many differences in technique, stimuli and theoretical background.

Today, neuroaesthetics is a rather heterogeneous research area: scientists have entered the field with different backgrounds, interests and questions in mind. Hence, there is not necessarily a consensus on what the important questions are or about how best to produce answers. The *Copenhagen Neuroaesthetics Conference* (held at the University of Copenhagen, September 24–26, 2009) provided a timely opportunity to reflect upon differences in the methods and results of recent studies, to address crucial unresolved issues and to synthesize a unified picture of our current understanding of the biological basis of artistic and aesthetic experience.

The conference broke new ground in several respects. First, the organizers—Søren Kaspersen, Jon O. Lauring, and Martin Skov—brought together over 25 researchers from a broad range of fields, including anthropology, philosophy, linguistics, art history, psychology, neuroscience and zoology, to present and discuss their research on neuroaesthetics. Second, the program was both broad and coherent, covering a variety of artistic forms (painting, literature, music, dance and film) and a range of humanistic, cognitive, neuroscientific, and evolutionary approaches. Third, the atmosphere invited attendants to exchange ideas and perspectives, and to contribute constructive criticism. Presentations were followed by short (and usually lively) discussions, which continued into coffee and lunch breaks, and there was a final session for general discussion at the end of the *Conference*. In the remainder of this paper we report some of the most groundbreaking contributions and fruitful discussions. As noted, our focus will be on those aiming to identify brain regions involved in aesthetic appreciation and its evolution. This selection includes presentations on appreciation of painting, music, dance, and human faces. We begin our report, though, with one of the most pressing issues: the definition of the field's scope and methods.[1]

4. What is neuroaesthetics?

One of the main issues raised at the *Conference* was the definition and scope of the field. Neuroaesthetics is often conceived as the study of the neural basis of the production and appreciation of artworks (Changeux, 1994; Nalbantian, 2008; Zeki, 1998, 2001; Zeki & Lamb, 1994). However, Brown and Dissanayake (2009) argued that because art goes beyond aesthetic concerns, this definition is too broad in that it attempts to account for the biological underpinnings of artistic behavior, which includes a number of cognitive and affective mechanisms that have no aesthetic relevance. Hence, they contend that in addition to neuroaesthetics, a field of neuroartsology is required. In contrast to this view, authors such as Skov and Vartanian (2009a) have used the term neuroaesthetics in a rather more general way to encompass the study of the biological roots of the variety of psychological and neural processes involved in the creation and perception of artistic and non-artistic objects. In this sense, neuroaesthetics is close to what Fitch, von Graevenitz, and Nicolas (2009) have defined as bioaesthetics.

We believe that at this stage of the field's development, a broad and inclusive definition is preferable. Accordingly, throughout this paper we use the term neuroaesthetics to encompass the study of the neural and evolutionary basis of the cognitive and affective processes engaged when an individual takes an aesthetic or artistic approach towards a (western or non-western) work of art (used in the broad sense to include music, film, theater, poetry, literature, architecture and so on), a non-artistic object or a natural phenomenon. Such a definition is broad enough to include the psychological and neural processes underlying, for instance, the assessment of a renaissance masterpiece by art experts (artists, art critics, art historians), the appreciation by non-experts of the same artwork, a decorative vase, a sports car, a pair of shoes in a window shop, a human face or figure, a flower, a sunset or a storm, the creation of artworks and designs, as well as the evolutionary processes that have conferred on our species such neural and psychological processes. This broad coverage and focus on psychological experience rather than a particular class of artefacts has the advantage of allowing research in neuroaesthetics to establish the effects of the artistic status or usage of objects, assessing the influence of individuals' background, and so on. It also allows researchers to draw upon a broad range of studies to frame and interpret their own results.

In his contribution to the *Copenhagen Neuroaesthetics Conference*, entitled *Visual neuroaesthetics: Principles and practice*, Anjan Chatterjee distinguished three complementary approaches for neuroscientists interested in aesthetic questions. The first and most basic is to propose theories about how artists might use an implicit understanding of the brain's perceptual systems to engage their audience in their work. The second approach goes beyond such observations to neuropsychological and clinical examinations of how disrupting brain function affects artistic creation and appreciation. The third approach seeks to actually test hypotheses about the neural basis of artistic appreciation and production, primarily using neuroimaging. Although Chatterjee believes the third approach to be the most scientifically sound, he notes that it makes the tacit assumption that complex artistic and aesthetic experiences result from the interaction of simpler processes whose contribution to aesthetic experience can be investigated separately. However, this may not be the case: it may be impossible to isolate the component processes without losing the aesthetic experience itself. Even the fact that almost all studies are performed in laboratories using specially designed stimuli, often artificially created or standardized in some way, is a strongly limiting factor. Outside the laboratory people can choose the context in which they wish to engage in aesthetic or artistic activities (the privacy of their homes, museums, concert halls, among others), the length of time they wish to do so and, most of the time, the music they wish to hear, the exhibition they wish to visit, and so on. So the question of ecological validity remains: are experiences elicited in the laboratory genuinely aesthetic experiences, and if so, can current methods really capture the essence of those experiences?

Several of the conference's participants presented the results of fMRI studies of participants performing aesthetic appreciation tasks. As in other areas of neuroscience, however, blobs of significant BOLD response tell us little unless one really understands their relation to the cognitive and affective processes involved in the specific task. Helmut Leder's contribution to the conference, *Why do we like art? Psychological explanations*, described a five-stage psychological model of aesthetic appreciation, and argued that it can function as an interpretative framework for neuroimaging and brain-damage studies.

The first of these stages is perceptual analysis, which is concerned with organization, grouping, symmetry analysis, complexity and other perceptual features that are known to influence aesthetic appreciation. In the second stage, the analysis of familiarity, prototypicality and meaning is performed, together with the implicit and automatic integration of information with pre-existing memory structures. Processes involved in explicit classification are performed in the third phase, including those related with the style and the content of the stimulus. Thereafter, in the cognitive mastering stage, the stimulus is interpreted on art-specific and self-related grounds. Finally, the model provides two different outputs: a cognitive state, product of the earlier cognitive stages, and an affective state, resulting from continuous interactions between the aforementioned processes and diverse affective mechanisms. The cognitive state provides the basis for aesthetic judgment, while the affective state generates emotional responses.

This model, which summarizes a considerable body of research within empirical aesthetics, highlights the complex interaction among many cognitive and affective processes that gives rise to

[1] Full details of all presentations and posters can be found at http://naconference.ikk.ku.dk/keynote/.

aesthetic experiences. Neuroaestheticians, thus, face the challenge of creating experimental designs that can tease apart the relations between activity in specific brain regions and specific cognitive and affective processes in aesthetic experience.

5. Insights from brain damage and degeneration

In her presentation, *Art, beauty, brain and neuropsychology*, at the conference, Dahlia Zaidel argued that neuropsychological evidence shows artistic skill and creativity to be surprisingly resistant to brain damage. Contrary to popular belief, there is no strong neuropsychological evidence for a right hemisphere specialization for visual art. Similarly, although music was once thought to be predominantly right-lateralized, it is now known to engage neural processes in both hemispheres (Levitin & Tirovolas, 2009). Zaidel's study of artists that suffered unilateral damage to the brain reveals that they could continue painting with the same style they had developed prior to the injury. The observable modifications to their technique seem to be due more to the limitations caused by the damage itself or attempts to adapt to it. Artists suffering from dementia also retained their artistic skill and style until the degeneration of cognitive faculties was all-pervasive. These observations contrast with those of Annoni, Devuyst, Carota, Bruggimann, and Bogousslavsky's (2004) who reported visible modifications in the style of two professional painters after a stroke. In fact, several studies have shown that various neurological conditions, including epilepsy, migraine, and different neurodegenerative diseases, had a significant impact on artists' work (Bogousslavsky & Boller, 2005; Rose, 2006). It has been argued that when the lesion is more localized, such as that caused by a stroke, the effects on artistic production are subtle and can be difficult to detect at all after the acute phase, whereas dementias and other more general conditions do tend to have visible effects (Bogousslavsky, 2005; Boller, Sinforiani, & Mazzucchi, 2005).

In some instances neurological disorders, far from hampering artistic production, can spark creativity – even in people with no prior inclination towards art. Miller, Boone, Cummings, Read, and Mishkin (2000) studied the painting and musical performance of patients suffering from left anterior frontotemporal dementia, affecting mainly their anterior temporal lobe, who sustained or appeared to acquire novel painting or musical skills. The authors described the paintings as lacking in abstract and symbolic features, they mostly depicted landscapes, people or animals that were either copied or remembered, or perfected visual designs. Mell, Howard, and Miller (2003) attribute this emergence of artistic talent to the release from the influence of the dominant language-related thinking usually exerted over the non-dominant posterior right temporal and parietal cortex, thought to play a role in accurate drawing. In contrast with prior descriptions of these patients' work, however, Rankin et al. (2007) later reported that paintings by patients with frontotemporal dementia were judged by an expert panel as bizarre, as often including abstracted or simplified images, containing few details, deviating from explicit and representational depictions, and suggestive of a spatial organization deficit.

It is clear from this brief overview that there is little agreement as to the nature and extent of the impact of neurological conditions on the production of art. In addition to the scarcity of these cases, the patients were affected by very different syndromes, at different ages, they were skilled to different degrees before being affected, and differed widely in terms of their educational and social backgrounds, and even basic demographic variables such as age and sex. Although elaborating meaningful general conclusions under these conditions is not an easy task, a systematic meta-analysis is clearly warranted.

Another problem derives from the lack of common measurement and interpretative instruments available to researchers. As clearly shown in Chatterjee's presentation at the conference, researchers have described the paintings created by brain-damaged patients using varied and imprecise terms, at different levels of generality, and attending to different features. In his contribution, Chatterjee presented a procedure developed precisely to overcome this difficulty, the Assessment of Art Attributes Test. This instrument has been designed to enable a standard appraisal of pictorial works created by patients before and at different stages after onset of their condition. The test includes quantitative measures of abstraction, balance, color saturation and temperature, complexity, depth, emotion, realism, stroke, or symbolism, among others (Chatterjee, Widick, Sternschein, Smith, & Bromberger, 2010). Such an instrument will facilitate comparisons across studies and allow researchers to move beyond vague and imprecise assessments of the impact of neurological conditions on artistic production.

Despite these limitations, there are some clear conclusions afforded by the kind of studies discussed above. Zaidel and Chatterjee's contributions summarized these conclusions, which are developed in detail elsewhere (Chatterjee, 2004b; Zaidel, 2005, 2010). First, neuropsychological studies have revealed that artistic and aesthetic experiences involve the participation of several brain regions. Second, there seems to be no clear hemispheric advantage for artistic or aesthetic activities, which does not preclude a certain degree of hemispheric asymmetry for cognitive or affective processes underlying such activities. Third, our capacity to create and appreciate aesthetic and artistic phenomena emerges from the interaction between processes of perception, memory, decision-making, emotion and attention.

6. The neuroimaging of visual aesthetics

6.1. Visual art

Edward Vessel's presentation, *This is your brain on art*, reported an fMRI study in which participants indicated how beautiful, compelling, moving or powerful they found artworks. The strength of the aesthetic experience correlated with activity in several temporal and prefrontal cortical areas involved in high-level sensory processing and judgment, as well as in subcortical regions related with reward, including the thalamus, the pontine reticular formation, and the caudate. There was greater activation in the medial frontal cortex, substantia nigra and hippocampus, while participants viewed their most liked artworks, compared to all other stimuli. Vessel argued that these regions play a special role in highly moving aesthetic experiences (see Table 1 below for a summary of neuroimaging results presented at the conference).

Martin Skov's presentation, *Evidence for a process theory account of aesthetic valuation*, covered several fMRI studies exploring the influence of expertise and contextual information on aesthetic experiences. In one study, his team presented photographs of buildings and faces to architects and non-architects, who indicated how appealing they found them. Activation in the medial orbitofrontal cortex increased with level of appeal for both groups, although the increase was greater for the group of experts when viewing buildings. Activation in the anterior cingulate cortex was also related with aesthetic ratings. Whereas such activation was similar for both groups of participants while rating faces, activation in this region increased for experts and decreased for non-experts when they rated buildings. Conversely, nucleus accumbens activation correlated with appeal irrespective of expertise and stimulus kind (see Kirk, Skov, Christensen, et al., 2009, for additional details).

In another study (Kirk, Skov, Hulme, et al., 2009), naïve participants were asked to rate the appeal of computer generated abstract paintings. Participants were told that some of the images they would see belonged to a renowned art museum and that

Table 1
Location of main brain activation reported in the *Copenhagen Neuroaesthetics Conference* presentations highlighted in this report.

Presenter	Stimuli	Prefrontal cortex	Other cortical regions	Subcortical regions
Vessel	Paintings	IFG, SFG, OFC, mPFC	Superior temporal sulcus Inferotemporal sulcus Collateral sulcus	Substantia nigra Hippocampus Caudate Thalamus Pontine reticular formation
Skov	Architecture	ACC, OFC mPFC		Ventral striatum
Ishai	Faces	OFC		
Calvo-Merino	Dance movements		Visual cortex Premotor cortex	
Koelsch	Music		Insula Rolandic operculum Temporal poles	Ventral striatum Amygdala Hippocampus
Brattico	Music	ACC, mPFC	Temporal poles	Ventral striatum
Jacobsen	Music and visual designs	IFG, mPFC		

ACC: Anterior cingulate cortex; IFG: Inferior frontal gyrus; mPFC: Medial prefrontal cortex; OFC: Orbitofrontal cortex; SFG: Superior frontal gyrus.

others had been created by the experimenter using a computer program. The results showed that medial orbitofrontal activation correlated more strongly with appeal ratings when participants were told that the paintings were exhibited in the museum, suggesting that this region is sensitive to the effect of expectations on hedonic value. Based on his research, Skov defended the conception of aesthetic values as the manifestation of a general system that motivates decisions about behavior. In this system, and in the psychological model presented by Leder, aesthetic judgments involve both bottom-up and top-down processing of a sensory object and are sensitive to context and to the prior experience of the observer.

6.2. Human beauty

In addition to visual art, the conference also covered a topic of special interest in visual neuroaesthetics: facial beauty. Other people's faces constitute highly relevant stimuli for humans, and face perception is mediated by distributed neural regions (Ishai, 2007), including the extrastriate cortex, which is specially dedicated to processing individual identity, and the superior temporal sulcus, which processes facial movements involved in speech and directing gaze. Regions of the limbic system, such as the amygdala and insula, are involved in recognizing facial expressions of emotion. Research during the last decade has revealed that facial beauty is processed by regions of the reward circuit, especially the nucleus accumbens and orbitofrontal cortex (Aharon, Etcoff, Ariely, Chabris, O'Connor, & Breiter, 2001; Kampe, Frith, Dolan, & Frith, 2001; O'Doherty et al., 2003), as well as ventral occipital cortex (Chatterjee, Thomas, Smith, & Aguirre, 2009).

Research presented by Alumit Ishai at the conference aimed to throw light on the role of gender and sexual orientation on ratings of attractiveness for male and female faces. Participants included heterosexual and homosexual men and women. The results showed that for heterosexual women and homosexual men, activation in orbitofrontal cortex was higher for attractive male faces than attractive female faces, whereas the converse was true for heterosexual men and homosexual women. According to Ishai, the orbitofrontal cortex represents the reward value of faces of potential sexual partners, rather than reproductive fitness. It should be noted, however, that the relationship between facial beauty and reward is not necessarily straightforward. Aharon et al. (2001) found that young, heterosexual males rated pictures of beautiful male and female faces as attractive but would exert effort to extend their viewing of the beautiful females only, suggesting that only these were rewarding.

Another presentation at the conference generalized the discussion from facial beauty to all aspects of human beauty. In his talk, *Darwinian aesthetics: Perfect faces, perfect bodies, perfect genes?* Karl Grammer reviewed the empirical evidence for the effects of facial symmetry, skin texture, body odor, voice and gait on the perception of beauty and how these effects are related to sexual selection. Female faces, for example, are rated as significantly more attractive during ovulation, and Grammer argued that this is because skin texture and color become more homogeneous and facial features more symmetrical. We return to the evolutionary aspects of Grammer's presentation below.

6.3. The appreciation of visual motion in dance

Although research in neuroaesthetics has tended to focus on visual art, independent research on music and dance is now beginning to make significant contributions to the field. In fact, several presentations at the conference focused on perception of visual motion in dance. This research is based on the neuroscience of body posture and movement perception, which has uncovered two specialized routes for processing human bodies. One of these, which involves areas of the dorsal visual system and the premotor cortex, seems to process bodies in a configural manner, and activate the observers' own sensoriomotor representations. The other route, which is part of the ventral visual processing stream, and includes the extrastriate body area, appears to be specialized in the processing of specific details of body posture (Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007).

One topic of special interest is the influence of motor expertise on action observation. Greater activation in premotor cortex, parietal areas, which have a somatotopical organization, and superior temporal sulcus, involved in biological motion perception, has been observed when expert dancers view movements corresponding to their own style compared to the other style (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008). Calvo-Merino, Ehrenberg, Leung, and Haggard (2010) showed that dance expertise enhances mainly configural, rather than featural, processing of dance movements.

Calvo-Merino's contribution to the conference, *Neuroaesthetics of performing arts: A sensoriomotor approach*, dealt with the neuroscience of movement from an aesthetic perspective. She reported an experiment in which short video clips of ballet movements were shown to ballet dancers and non-dancers during MRI acquisition. The stimuli were presented in pairs and participants were required either to indicate whether the movements were the same or different, or to choose which they liked most. The results revealed that the preferred dance movements elicited greater activation in premotor cortex, especially for experts, suggesting that aesthetic preference for dance involves an enhanced cortical representation of those movements. The second experiment reported by Calvo-Merino was designed to determine the relative contribution of the two body-processing streams identified by Urgesi et al. (2007). In this study, they used transcranial magnetic stimulation over the dorsal and ventral pathways while participants rated how much they liked various dance postures. Results showed that the procedure interfered with aesthetic appreciation especially when applied over the dorsal pathway, that is, the one involved in configural processing. This suggests that the general configural aspects of dance have a stronger effect on aesthetic appreciation than the specific features of body postures.

7. Neuroaesthetics of music

There is emerging evidence that distinct neural structures subserve the perception of many different musical attributes, including pitch features (absolute pitch, pitch interval, contour), temporal features (e.g., rhythm, meter, tempo), loudness, timbre and spatial location (Levitin & Tirovolas, 2009; Peretz & Zatorre, 2003). For example, pitch processing appears to be based on tonotopic representations in primary and secondary auditory cortices and there is evidence that distinct cortical regions process pitch interval and pitch contour (Liégeois-Chauvel, Peretz, Babaï, Laguitton, and Chauvel, 1998; Stewart, Overath, Warren, Foxton, & Griffiths, 2008). There is also some evidence for a distinct auditory 'where' pathway in posterior auditory and inferior parietal cortex encoding the spatial location of sounds (Zatorre, Bouffard, Ahad, & Belin, 2002; Scott, 2005). Research with Parkinson's patients converges with neuroimaging data to suggest that the basal ganglia play a crucial role in the perception of a metrical beat in music (Grahn, 2009).

Modular models of the neural processing of music (Koelsch & Siebel, 2005; Peretz & Coltheart, 2003) propose that the representations created by perceptual analysis are passed onto limbic and paralimbic emotional systems including both cortical and subcortical structures. The latter include the amygdala, nucleus accumbens and parahippocampal gyrus while regions in the frontal cortex, especially the orbitofrontal and ventromedial prefrontal cortex are also thought to be key to the emotional processing of music (Peretz, 2010).

The affective valence of music is thought to be influenced in part by tempo and mode such that slow, minor-key music is associated with negative emotions and fast major-key music is associated with positive emotions (Khalfa, Schön, Anton, & Liégois-Chauvel, 2005). Neuroimaging research has associated positively-valenced responses to classical music with activation in the bilateral ventral and left dorsal striatum, left anterior cingulate and left parahippocampal gyrus, while negatively-valenced responses with activation in the hippocampus and amygdala (Mitterschiffthaler, Fu, Dalton, Andrew & Williams, 2007). Emotional responses to music are central to neuroaesthetics research and were covered by several presentations at the conference.

Andrea Halpern's contribution, *Major–minor perception by musicians and non-musicians*, presented a series of experiments examining the relationship between major and minor keys and the experience of happiness and sadness in music. While musicians easily distinguish between major and minor keys, non-musicians do not unless the words 'major' and 'minor' are replaced by 'happy' and 'sad'. However, in an ERP study, only musicians produced a strong electrophysiological response to the first note in a melody that distinguishes it as minor but not to the major equivalent, suggesting that they were recruiting distinct neural processes from non-musicians. Many questions remain about the role of tempo and mode in generating musical emotions. It is unknown, for example, to what extent these are universal associations or culturally determined through experience. The issue of whether listeners actually feel the emotions they attribute to music or whether they are simply assigning emotional labels to particular kinds of music also remains open. It is important that future research investigates the development of emotional responses to music and also the emotional responses of non-Western listeners to address these questions and identify other determinants of valence in musical responses. It is also important to determine other features of music that reliably generate particular emotional responses and understand why they do so.

A complementary approach to studying the neural basis of emotional responses to music is to leave aside the question of which musical features generate emotional responses and simply rely on listener's self-reported emotional ratings to identify musical stimuli that generate different emotional responses. Mitterschiffthaler et al. (2007) took this approach but didn't control for preference for their musical stimuli. At the conference, Elvira Brattico presented research which examined for the first time how happiness and sadness conveyed by music interact with its aesthetic effects. In her talk, *The neural correlates of the aesthetic experience of music*, she reported an fMRI experiment in which participants self-selected happy and sad pieces of music that they liked or disliked. Preferred music activated limbic and paralimbic regions, including cingulate cortex, ventromedial prefrontal cortex and ventral striatum, whereas the emotional content of music differentially activated temporal lobe structures.

A second strand of research on emotional responses to music has examined they way in which music stimulates arousal. This was the topic of a presentation by Stefan Koelsch at the conference addressing the question *What makes music pleasant and unpleasant?* The theoretical groundwork for research in this area was laid down by Meyer (1956) who proposed that music sets up expectations for what is to come next; confirmation and violation of these expectations generate an experience of tension and resolution which produces emotional responses. Listeners' expectations reflect the probabilities of musical events occurring suggesting that they are tuned through experience to provide good predictions of the environment (Pearce & Wiggins, 2006). As a result, confirmations of musical expectation are often rewarding. However, somewhat paradoxically, violations of expectation may also be pleasurable possibly due to the contrast between the initial startle of surprise and its subsequent appraisal as innocuous (Huron, 2006).

Huron (2006) has suggested that violations of expectation in music produce characteristic emotional and physiological responses related to fight, flight or freeze responses to environmental danger. This is supported by the recent finding that violations of pitch expectation in melody generate patterns of beta band activation characteristic of auditory-motor synchronization (Pearce, Ruiz, Kapasi, Wiggins, & Bhattacharya, 2010). Empirical research with EEG has demonstrated that unexpected chords in music produce characteristic electrophysiological responses and higher arousal indicated by galvanic skin response (Steinbeis, Koelsch, & Sloboda, 2006). Another kind of physiological response to violations of musical expectation is frisson: the shivers or 'chills' that some people experience in response to some pieces of music (Grewe, Kopiez and Altenmüller, 2009; Huron, 2006; Sloboda, 1991). Chills are a common and pleasurable physiological response to music (Grewe et al., 2009) and produce changes of activation of brain regions such as the ventral striatum, orbito-frontal and ventromedial prefrontal cortex, and amygdala which are associated with reward (Blood & Zatorre, 2001). The involvement of reward-related areas in aesthetic responses to music is consistent with the findings of research with visual art.

In Copenhagen, Koelsch also discussed another feature that is capable of generating pleasurable and displeasurable responses to music: consonance and dissonance. Previous research has found that orbitofrontal, cingulate, and frontopolar cortices mediate the experience of pleasant consonant music (Blood, Zatorre, Bermudez, & Evans, 1999). Koelsch reported an fMRI study designed to determine the neural correlates of listening to pleasant and unpleasant music (Koelsch et al., 2006). Whereas Blood et al. (1999) used computerized sounds as stimuli, Koelsch used fragments of joyful instrumental tunes as well as continually dissonant counterparts of these fragments. Participants without musical training or education were asked to listen carefully to the music while tapping to the beat, and then indicate how pleasant or unpleasant they felt. The results showed that while dissonant music activated structures related to processing negatively valenced stimuli (amygdala, hippocampus, parahippocampal gyrus and temporal poles), consonant music activated areas such as the insula and rolandic operculum, involved in vocal sound production, as well as the ventral striatum. These results reveal that the perception of pleasant music is mediated by reward circuitry as well as a perception–execution system representing vocalizable auditory information.

These neuroimaging results have found corroboration in neuropsychological research. It has been shown, for example, that patients with lesions to the parahippocampal gyrus rate dissonant musical excerpts as pleasurable although they are unimpaired on judgements of emotional valence (Gosselin et al., 2006). Damage to the amygdala, on the other hand, impairs the recognition of negatively valenced music (scary and sad) while sparing the perceptual discrimination of happiness and sadness in music (Gosselin, Peretz, Johnson, & Adolphs, 2007).

8. Neural basis of aesthetic experience

In bringing together the results of the presentations highlighted in this paper, it becomes clear that aesthetic and artistic activities typically involve a network of brain regions distributed over both hemispheres, rather than a specialized area. Functional analysis of these regions suggests that aesthetic appreciation of painting, music and dance involves at least three different kinds of measurable brain activity: (i) An enhancement of low-level cortical sensory processing; (ii) high-level top-down processing and activation of cortical areas involved in evaluative judgment; (iii) an engagement of the reward circuit, including cortical (anterior cingulate, orbitofrontal and ventromedial prefrontal) and subcortical (caudate nucleus, susbtantia nigra, and nucleus accumbens) regions, as well as some of the regulators of this circuit (amygdala, thalamus, hippocampus).

A number of published papers have reported activation of high-level sensory cortex while participants rated different aesthetic dimensions of images. Activity in occipital cortex related with positive aesthetic experiences was identified by Cupchik et al. (2009) and Vartanian and Goel (2004), in temporal cortex by Jacobsen et al. (2006), Lengger et al. (2007) and Yue et al. (2007), and in parietal cortex by Cela-Conde et al. (2009), Fairhall and Ishai (2008), and Lengger et al. (2007). Koelsch and Calvo-Merino's presentations at the conference, revealed that this aspect of aesthetic experience generalizes to music and dance. Liking of musical fragments and dance sequences is correlated with activity in brain regions related with the perception of sound and body movement.

Published neuroimaging studies have also identified activity related with evaluative judgment and attentional engagement associated with aesthetically pleasing visual stimuli. Activation in lateral prefrontal cortex was identified by Cela-Conde et al., 2004, Cupchik et al. (2009), Jacobsen et al. (2006), and Lengger et al. (2007), and in medial frontal cortex by Jacobsen et al. (2006).

Several studies have reported activation in regions related with different aspects of affect and emotion while participants viewed images or listened to musical fragments they rated as beautiful. These regions are constituents of what is known as the reward circuit or its modulators (Kringelbach & Berridge, 2009). Orbitofrontal activation, presumably related to the representation of reward value, was identified by Blood et al. (1999), Blood and Zatorre (2001), Cupchik et al. (2009) and Kawabata and Zeki (2004). Anterior cingulate activation, possibly reflecting monitoring of one's own affective state, was identified by Blood et al. (1999) Cupchik et al. (2009) and Vartanian and Goel (2004). The involvement of subcortical components of the reward circuit in aesthetic experiences has been reported by Cupchik et al. (2009), Di Dio et al. (2007), Gosselin et al. (2007), Mitterschiffthaler et al. (2007), Vartanian and Goel (2004), and Yue et al. (2007).

Although evidence supporting this view of the neural mechanisms underlying aesthetic appreciation seems to be accumulating, a number of issues are raised by the findings reported in these studies and the discrepancies among them. There are at least two pressing issues. First, what factors are responsible for the observed discrepancies in the results of the studies reviewed above? For instance, although several studies report enhanced high-level perceptual processing, different studies have identified the enhancement variously in occipital, temporal or parietal cortices. Nadal, Munar, Capó, Rosselló, and Cela-Conde (2008) have suggested that some of these discrepancies could be explained by the different kinds of stimuli used, different proportions of male and female participants, different procedures and techniques, and even different instructions and tasks to register aesthetic responses. Recent research has shown, as might be expected, that representational stimuli engage neural mechanisms involved in object perception much more strongly than abstract stimuli (Fairhall & Ishai, 2008). Equally, Cupchik and colleagues (2009) have demonstrated the effects of instructions on brain activity related with aesthetic appreciation. Further systematic research is required to clarify the influence of these and other factors on the neural underpinnings of aesthetic appreciation.

Second, it is becoming increasingly clear that psychological models (Chatterjee, 2004b; Leder et al., 2004) have underspecified affective processes involved in aesthetic appreciation. Some studies have identified activation in emotion-related brain regions, such as the insula (Cupchik et al., 2009; Di Dio et al., 2007), others have identified activation in regions thought to be involved in coding reward value, such as the orbitofrontal cortex (Kawabata & Zeki, 2004; Vartanian & Goel, 2004), and others have reported activation in pleasure generating subcortical regions (Yue et al., 2007). Furthermore, the results reported by Skov at the conference (see also Kirk, Skov, Christensen, et al., 2009; Kirk, Skov, Hulme, et al., 2009) have clearly shown that orbitofrontal cortex, anterior cingulate cortex, and nucleus accumbens play distinct roles in aesthetic appreciation. The studies presented by Skov and Ishai at the conference took into account the variables of expertise, context, and sexual preference. Their results, which showed that activation in the orbitofrontal cortex was modulated by those factors, indicate that this region may compute reward values resulting from integrating core hedonic responses to the stimulus with contextual and personal information. Conversely, subcortical components of the reward circuit seem to be relatively unaffected by modulating factors and may be responsible for the pleasurable aspect of aesthetic experiences. Skov's presentation showed that the activity of the nucleus accumbens, an essential component of the reward circuit, was unaffected by people's prior experience with the materials they were rating. These findings pose a challenge to researchers to develop ingenious experimental designs to clarify the role of different brain regions involved in aesthetic appreciation.

Finally, it is interesting to ask to what extent these neural responses to diverse artistic forms, such as music, painting and dance, among others, might reflect domain general emotional or aesthetic processes. In his contribution to the conference, entitled *Aesthetic judgments of beauty*, Thomas Jacobsen compared responses to visual art and music, and presented evidence from two separate fMRI studies of aesthetic responses to visual and auditory stimuli (Jacobsen et al., 2006; Kornysheva, von Cramon, Jacobsen, & Schubotz, 2010), noting that in both cases, aesthetic judgments generated greater activation in antero-medial and inferior frontal gyrus than was produced by control tasks (visual symmetry and auditory tempo judgments), suggesting a modality-independent system for the judgment of beauty. The identification of modality-independent neural substrates of aesthetic experience is an important topic for future research in neuroaesthetics.

9. An evolutionary perspective

In addition to asking about the neural foundations of our aesthetic experiences, neuroaesthetics also seeks to understand their evolutionary history. The evolutionary origins of our capacity to produce and appreciate beautiful art puzzled early Darwinian thinkers, who attempted to determine the selective advantage conferred by such a trait. Today there is still much disagreement about the adaptive significance of art and aesthetic experiences. In one approach, artistic behaviors are viewed as exaptations, exemplified by Steven Pinker (1997) who famously suggested that music is "auditory cheesecake". Our preference for cheesecake derives from an evolved preference for the fats and oils that were advantageous to survival in the moderate quantities naturally occurring in nuts and seeds but are disadvantageous to survival in the unlimited quantities available to us today in artificially produced cheesecake. Pinker argues that music is a by-product of cognitive and behavioral functions adapted for language.

Others have argued that art and aesthetics have had a clear adaptive value. But what selective advantage might aesthetic activities confer? Darwin himself, for example, suggested that music, like birdsong, might have evolved through sexual selection to support mate choice. Acquiring the skills to produce high quality works of art is difficult, rare and costly, so the ability to do so might serve as an honest signal of such qualities as health, energy, creativity, access to rare materials, good learning abilities, intelligence and coordination, among others (Miller, 2001).

Visual aesthetic preferences have also been linked to habitat selection, assessing environments to make decisions about where to move and settle, which is assumed to have been especially important to our Pleistocene ancestors who were nomadic hunter-gatherers (Kaplan, 1987; Orians & Heerwagen, 1992). Our aesthetic preferences reflect evolved preferences for habitats with features characteristic of a high-quality tropical African savanna.

Two presentations at the *Copenhagen Neuroaesthetics Conference* took an evolutionary perspective on neuroaesthetics. The argument presented by Ellen Dissanayake in her talk *Proto-aesthetic responses in hominins of the early Pleistocene,* began by noting that the narrowing of the pelvis to facilitate bipedalism and the increased brain size in erectus-grade hominins, which occurred about 1.8 million years ago, led to a shorter gestation period. Natural selection then favored strategies used by mothers to provide necessary additional care during the ensuing altricial period. The signals used by adults to communicate with infants are simplified or stereotyped, repetitive, exaggerated, elaborated in visual, vocal and kinesthetic ways. These features engage the infant's attention and generate states of anticipation and expectation. Dissanayake argued that these strategies served as a pool from which later hominins could draw when they began to carry out artistic and ritual activities. In fact, these attributes constitute essential components of ritualization and artification behaviors observed in all human societies.

Although Dissanayake's views are consistent with what is known about art in traditional non-western societies, and overcomes some of the drawbacks of other proposals, her approach is still hypothetical. Given the lack of fossil and archaeological evidence for many of the proposed cognitive processes, it is almost impossible to derive empirically testable predictions from the theory. This remains a critical challenge for Dissanayake's work and for adaptive accounts of aesthetic behaviors in general which must not degenerate into post hoc 'just-so' stories (Fitch, 2006).

Precisely such a transition from evolutionary theory to hypothesis testing was the focus of Karl Grammer's presentation, discussed above. Grammer reviewed how features known to influence human beauty, such as averageness, symmetry and sex-hormone markers, are expressed in facial and body form, skin texture, body motion, body odor, voice, and hair, and how these traits are related with genetic and developmental factors. Grammer also addressed the question of how receivers of fitness signals arrive at a coherent assessment based on such a multiplicity of cues. He argued against the proposal that each feature signals different aspects of mate value, arguing instead that humans combine many different signals to derive a single estimate of mate fitness that is more reliable than any of its components. Finally, Grammer argued against the existence of innate beauty detectors for particular representational content, proposing instead a set of innate abstract rules for constructing beauty templates through experience.

10. Future challenges for neuroaesthetics

If the *Copenhagen Neuroaesthetics Conference* had a single shortcoming, it was the limited time for questions and debate after each of the presentations, which is so important for opening dialogues between scholars with such different backgrounds. As a result, there was not enough opportunity to reach an explicit consensus for establishing key founding principles and priorities for research in neuroaesthetics, or to deal with some of the most frequent criticisms aimed at the field. We have attempted to specify what we believe to be some foundations for such a synthesis in previous pages. These foundations are not necessarily exhaustive and we expect them to be revised and strengthened with further research. In doing so, the field must listen to its critics, identify and address those challenges that, if ignored, could become serious pitfalls.

10.1. Challenges related with the field's internal coherence

One issue that requires immediate attention is the extent to which neuropsychological and neuroimaging results converge. The literature reviewed in this paper suggests that there is no simple correspondence between the two approaches. This is partly because most studies of the relation between art and brain lesions and degeneration have concerned the production of art, while most neuroimaging studies have attempted to identify brain activity related to the appreciation of artworks or designs. Another issue that requires close attention is how neuroscientific and evolutionary perspectives can contribute to each other. Evidently, knowledge about the evolution of aesthetic appreciation is relevant to understanding its neural foundations, and vice versa, but the precise ways in which the relationship can be best exploited are currently far from obvious. Thus, neuroaesthetics faces the challenge of providing an account of aesthetic and artistic activities that integrates results from neuroimaging, neuropsychology and evolution.

10.2. Methodological challenges

Have neuroimaging studies really registered neural activity related with aesthetic appreciation? To our knowledge none of the studies presented in this review have included experimental control of – for instance – attentional mechanisms, and very few have attempted to control for the affective value of the stimuli. Thus, it remains a possibility that some of the results we have summarized here reflect processes that are unrelated to aesthetics, and that, unbeknownst to researchers, their participants were actually performing an attentional task, or an affective discrimination task, instead of an aesthetic appreciation task. Future work needs to develop methodological procedures aimed at identifying and controlling the effects of attention and affective value of stimuli, among other possible confounding factors, during aesthetic appreciation. And the same can be said of lesion and brain degeneration studies which, to date, have for the most part been unclear as to the precise cognitive processes affected and the scope of the impairment, and have rarely been accompanied by a comprehensive neuropsychological assessment of the people in their samples.

Chatterjee (2011) has noted two methodological issues that are even more problematic. First, by their experimental nature, scientific approaches to aesthetics involve quantification and decomposition. Experiments in empirical aesthetics and neuroaesthetics usually require participants to use some sort of rating scale to quantify some dimension of their reaction to the presented stimuli. The validity of such a strategy rests on the supposition that aesthetic experience can be meaningfully decomposed and quantified, that quantitative measures capture the essence of the aesthetic experience, and that they do not, in fact, interfere with it. However, the extent to which beauty, liking or preference ratings are good characterizations of aesthetic experience remains uncertain. Chatterjee (2011) eloquently points to this pitfall: "Reducing components of aesthetics to quantifiable measures risks inviting the proverbial problem of looking for the dropped coin under the lamp because that is where things are visible, even if the coin was dropped elsewhere" (Chatterjee, 2011).

The second methodological challenge identified by Chatterjee (2011) is to avoid relying on the reverse inference, that is, taking brain activity as an indicator for the engagement of a specific cognitive process. The field of neuroaesthetics has grown substantially owing to a number of neuroimaging studies. However, in many cases these studies have inferred the engagement of certain cognitive or affective operations while participants were performing aesthetic-related tasks in the scanner from identified brain activity. This would not be a problem if the active brain region were known to be involved only in one cognitive process. However, with very few exceptions, this is not the case. Brain regions are recruited to participate in a variety of cognitive processes. Poldrack's (2006) analysis suggests that "caution should be exercised in the use of reverse inference, particularly in cases where the prior belief in the engagement of a cognitive process and selectivity of activation in the region of interest are low" (Poldrack, 2006, p. 63). He does note, however, that reverse inference can constitute a rich source of new hypotheses that can be subsequently tested in other experiments. Bourgeois-Gironde (2010) provides strategies to establish relations between cognitive processes and brain activity in the field of neuroeconomics without having to rely heavily on reverse inference. Similar approaches should be considered to avoid neuroaesthetics repeatedly stumbling into this particular trap.

10.3. Challenges related with the identity and scope of the field

"Neuroaesthetics is a young enough field that there seems to be no established view of its proper subject matter", wrote Brown and Dissanayake (2009, p. 43). Disagreement among presenters and discussants at the conference as to what the main topic of neuroaesthetics should be and the specific issues it should address would seem to attest to such an assertion. There was also some disagreement as to the questions neuroaesthetics is not well suited to deal with. Probably the main unresolved matter is whether neuroaesthetics should be limited to aesthetic experience or whether it should – or can – address artistic activities too. We identify in the literature four reasons to argue that neuroaesthetics is not fit to address the arts: its almost exclusive focus on aesthetics; its search for the general over the particular; its de-contextualized approach; and its reduction of artistic experiences to neurobiological mechanisms.

Regarding its emphasis on aesthetic phenomena, Brown and Dissanayake (2009) have explicitly stated that neuroaesthetics is not well suited to deal with the whole sphere of art: "Aesthetic emotions are unquestionably an integral part of the arts, but they are neither necessary nor sufficient to characterize them. Thus, a narrow focus on aesthetic responses is ultimately a distraction from the larger picture of what the arts are about" (Brown & Dissanayake, 2009, p. 54). Beauty is of little relevance to many manifestations of art around the world and throughout history, which may have been created to intimidate, induce sorrow, to show a community's grandeur, to make us reflect on our own existence, and so on. Indeed, contemporary western art includes many instances of works that were explicitly conceived as a reaction against the concept of beauty. Furthermore, a given artwork often serves a multitude of purposes for different people, in different contexts, at different times. Can neuroaesthetics grapple with the emotional, formal, cultural, and intentional complexity inherent in the production and perception of the arts? In taking a broad view of aesthetics, as we have here, there is a rich seam to be mined in drawing links between neuroaesthetics and long traditions of empirical research in the psychology of music and visual art.

There is also the question of whether neuroaesthetics can tell us anything new about particular works of art. Massey (2009) argues that it cannot: "Neurology is, then, of great value in exploring the 'how' of aesthetic processes, if not necessarily the 'why' or the 'what for,' or in helping to decide whether one work of art is of greater value than another" (Massey, 2009, p. 18). Tallis (2008a) goes further in dismissing neuroaesthetics as an extreme expression of "the faith of neuroscientism" (belief that the contents of human consciousness can be explained in terms of neural activation): "[Neuroaesthetics] casts no light on the specific nature of the objects and experiences of art or the distinctive contribution of individual artists. Nor does it offer any basis for the evaluation of art as great, good, or bad. In short, neuroaesthetics bypasses everything that art criticism is about" (Tallis, 2008a, p. 19). While this might be a defensible critique at present, it is perhaps not surprising that a field of endeavor still within its first decade has yet to address major questions that have occupied researchers in philosophical aesthetics and the humanities for hundreds of years. Conversely, it seems likely that empirical aesthetics as a whole has much to gain from greater interaction with its philosophical cousin.

Neuroaesthetics is also charged with de-contextualizing stimuli and participants. Given the procedural constraints imposed by neuroimaging methodology, experimenters have tended to present long successions of stimuli, with little contextual information, to large groups of participants. The environment is often less than conducive to aesthetic experience and we seek effects that we can generalize reliably and confidently to a population of individuals. "Paintings are treated as mere isolated stimuli or sets of stimuli. [...] The works and our experiences of them are divorced from their cultural context, and from the viewer's individual history" (Tallis, 2008a, p. 20). These issues certainly present challenges to which we return to below when considering the external validity of the field.

Finally, it has been argued that aesthetic experience cannot be reduced to an explanation in terms of neurobiological mechanisms involved in many activities completely unrelated to art, some even shared with other animals. In doing so one fails to explain what distinguishes the characteristically human experience of great works of art from everyday perceptual experiences: "Tickling up the mirror neurones does not explain why Donne's stanzas should have the particularly intense effect they (sometimes) do" (Tallis, 2008b). There is a legitimate debate to be had about the veracity of this statement but, whatever the outcome, it is undeniable that Donne's stanzas would have no effect whatsoever were it not for the activity of neurons and neurotransmitters in particular brain networks of a particular reader. As neuroscientists, it behooves us to investigate these necessary biological conditions for aesthetic experience. The question is to what extent these investigations can be informed by, and contribute to, questions raised about the arts in humanities research.

Can neuroaesthetics, with its reductionist scientific approach, make any headway in understanding art? We believe that a positive answer to this question can only be possible if neuroaestheticians accept the fact that if they reduce aesthetic experience to simplified decontextualised laboratory tasks, they cannot expect results obtained over a population of individuals to a collection of artworks to predict – and explain – every possible aesthetic experience outside of the laboratory. Advances in neuroaesthetics have been hampered by grand claims that most art can be accounted for largely in terms of the operation of specific neural mechanisms (Hyman, 2010). The fact that researchers are now able to identify the activation of brain regions during the experience of a work of art is certainly not the end of the story. We have only begun to scratch the surface and the issues reviewed above must certainly be borne in mind when digging deeper.

10.4. Challenges related with the field's external coherence

Given neuroaesthetics' interdisciplinary nature, a conscious effort is required to establish fluid interactions with neighboring disciplines. While relations with psychology, neuroscience and evolutionary biology are more or less functional, the relation between neuroaesthetics and the traditional humanities (aesthetics, art theory, musicology, literary criticism and so on) can be somewhat strained, on account of important discrepancies between their approaches: "the aesthetic and scientific approaches to describing the arts represent two different kinds of thinking" (Massey, 2009, p. 22). On the one hand, the scientific approach to aesthetics, whether in the tradition of Fechner and Berlyne's empirical approach or in the form of more more recent developments in neuroaesthetics, usually seeks to develop and test general hypotheses which can predict responses across individuals, contexts and experiences. On the other hand, studies in the humanities often focus on detailed formal, stylistic, iconographic and critical aspects – among others – of a particular work that afford the educated reader a full appreciation of the author's analysis. In this approach, there may be many valid ways of experiencing a work of art and to average out differences between individuals so as to maximize the commonalities would be to lose what makes a particular analysis unique and distinctive.

Also empirical aesthetics and neuroaesthetics aim for objective analysis: making observations that can be reproduced and verified intersubjectively. However, the subjectivity of individual experience (many aspects of which are yet to be fully understood in psychological and neural terms) is the very essence of the humanistic exploration of art and aesthetics. According to Massey (2009), science is unable, in principle, to access aesthetic experience because "Immersion in the phenomenology of an experience, even for the purpose of thinking about it, rules out the distance implied by a scientific perspective, with its pragmatic, experimental, or mathematical criteria of value." (Massey, 2009, p. 185).

Research in neuroaesthetics must examine whether the general-particular and objective-subjective barriers are insurmountable in principle, or whether they can be overcome. The best we can say at present is that we see these barriers and are trying to peek over them.

10.5. Challenges related with the field's future research avenues

In addition to the many issues already raised throughout the paper, one of the future directions neuroaesthetics must explore is the time course of brain activation related with aesthetic experiences. Researchers need to move beyond mere localization of brain areas engaged in such experiences to produce a dynamic view of neural processes. This is almost self-evidently true in the case of music and dance but also applies to the appreciation of visual art and architecture. Another important issue for future research is the identification of genuine modality-independent processes – distinct from modality-specific ones – involved in artistic and aesthetic appreciation involving different sensory modalities, such as music, dance, painting, and so on. Finally, a range of different approaches including developmental, comparative, cross-cultural and neurobiological methods must be taken to develop an empirical understanding of the evolutionary origins of artistic and aesthetic behaviors.

11. Final remarks

Any flourishing field of scientific endeavor must have a regular forum to allow researchers to meet and debate directly: the *Copenhagen Neuroaesthetics Conference* fulfilled this role admirably. Here we have tried to summarize the main themes of the conference and put them in a broader context by sketching out a framework for understanding neuroaesthetics research in terms of its historical background, scope and methods. We have attempted to synthesize from the existing state of knowledge some foundational principles for the field and some key pitfalls and challenges for future research.

The exchange of ideas in this new but blossoming field has also benefited greatly from Skov and Vartanian's (2009b) volume *Neuroaesthetics*, a broad compendium of thoughtful – and often thought-provoking – chapters addressing many of the field's crucial issues. For a young field facing many exciting challenges, there is no doubt that both conference and book will be regarded as foundation stones of neuroaesthetics in years to come.

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