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THE NEURAL CORRELATES OF AESTHETIC APPRECIATION

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Abstract

In everyday life, people all over the world come across art in some way, and the question of what constitutes an aesthetic experience has long been an interesting topic for humanistic and philosophical studies. Recently, neuroscientists have begun pinning down the neural correlates of artistic production and appreciation, sparking a whole new subfield within cognitive neuroscience, known as neuroaesthetics. Most studies have focused on the relationship between brain mechanisms and the appreciation of visual art, which has shown to be a meaningful and interesting complement to empirical aesthetics and psychology. By means of several modern measuring instruments and tools such as functional magnetic resonance imaging and magnetoencephalography, neuroscientists have successfully been able to observe specific brain activity in relation to specific aesthetic activities, such as viewing paintings or artworks. In this thesis, the supposed neural correlates of aesthetic appreciation are examined through critical investigations, where evidence from some of the more outstanding studies is reviewed and compared, as well as the different problems and complexities that the field is dealing with. Furthermore, the evolutionary history of aesthetic experiences and philosophical theories on aesthetics are also examined, as well as how certain neural deficits affect our cognitive and emotional abilities to appreciate art. The findings demonstrated in this thesis show that aesthetic appreciation is a multifaceted phenomenon, depending on specific neural interactions between bottom-up sensory processing areas, reward-related subcortical structures and top-down cortical processing areas, that all together form the experience of enjoying artworks across different sensory modalities.

Keywords: aesthetic appreciation, visual art, aesthetics, neuroaesthetics

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Introduction

Humans have spontaneously produced and enjoyed art for thousands of years, and still do so today. We paint objects to make them look more beautiful and appealing. We engage ourselves in aesthetic activities and invest our emotions into crafting objects with aesthetic value, for the sake of creating something that is simply beautiful to *us*. Producing and enjoying artworks, whether it is paintings, sculptures, crafts or similar things is something that all cultures have examined, but most often from a humanistic and subjective view (Cela-Conde, Agnati, Huston, Mora & Nadal, 2011). Since art and aesthetics are meaningful activities in their own right and are natural activities for the majority of people in all cultures, it may seem as enough reason that such universal and historically old human concepts should also be interesting for, and be subjected to, the neurobiological and psychological sciences (Pearce et al., 2016). In the field of cognitive neuroscience, researchers have recently begun to investigate the neural networks and intrinsic connections in the brain that supposedly make up for aesthetic experiences. This particular subfield is called neuroaesthetics, and its main objective has been to define the neural underpinnings of artistic activities and aesthetic experiences (e.g. Nadal & Pearce, 2011; Cela-Conde et al., 2011). The majority of the research within neuroaesthetics is confined to visual art but there are also other topics such as music and dance that are currently being examined, as well as other aesthetic activities (Cela-Conde et al., 2011). However, aesthetic appreciation of visual art also requires some understanding about the evolutionary origins of these aesthetic experiences, i.e. how and why these types of experiences exist at all (Zaidel, Nadal, Flexas & Munar, 2013). This is an interesting aspect of neuroaesthetics and therefore minor connections to evolutionary psychology will be made throughout this thesis.

An important development currently taking place in neuroaesthetics is the endeavor to understand how the appreciation of parts in a harmonic composition might come about, i.e. how the neural mechanisms work to put parts into a whole, in visual art and in other forms of art, as well. A growing body of evidence suggests that the neural foundations of aesthetic appreciation seem to point to certain interactions between the cognitive functions of the prefrontal cortex and the emotional functions of the limbic system (Changeux, 2012), involving the amygdala and the insula **(**Di Dio, Macaluso & Rizzolatti, 2007**)** as well as structures in the reward-circuit (Vartanian & Goel, 2004; Vessel, Rubin & Starr, 2009). Furthermore, as revealed by means of functional magnetic resonance imaging (fMRI), other recent research has shown that the left superior parietal lobule is involved in visuo-spatial exploration of aesthetic objects, and that the left lateral prefrontal cortex is involved in aesthetic orientation, suggesting that aesthetic experiences are mediated by top-down and bottom-up perceptual features via subcortical systems (Cupchik, Vartanian, Crawley & Mikulis, 2009). It has also been shown (Vartanian & Goel, 2004) that certain brain areas, such as the right caudate nucleus, decreases in activity in response to decreased preferences for paintings. In studies where patients have suffered from neurological deficits that affect the emotional aspect of enjoying music such as ‘musical anhedonia’ (a neurological disorder which makes the patient unable to experience any emotions while listening to music), various findings have suggested that the emotional processing of music seems to rest on different neural pathways (Griffiths, Warren, Dean & Howard, 2004; Satoh, Nakase, Nagata and Tomimoto, 2011), which might tell us valuable information about the processing of emotional stimuli, whether it be music or visual art.

Some philosophers have shown certain skepticism about whether or not science can reveal anything significant about art (Holt, 2013). Although studies in this fairly new subfield of cognitive neuroscience have shown several indications of how the brain processes aesthetic information, there are still conceptual, philosophical and methodological problems to consider. One problem is that when conducting studies on enjoyment of visual artworks (such as preference rate among different paintings), the artworks are often taken out of their cultural and historical contexts (Tallis, 2008; Zaidel et al., 2013). Isolating artworks from their cultural, historical and personal contexts is problematic for experimental aesthetics because they need to be taken into account and are essential for the evaluation of an aesthetic object. Zaidel et al. (2013), among some, have also proposed the crucial importance of a general framework within neuroaesthetics that is interdisciplinary, working across fields such as art theory, philosophy, archaeology, aesthetics and neuroscience. The abovementioned problems and more, such as the diffuse definitions of art and aesthetics and the scope of interest in neuroaesthetics, will all be addressed and reviewed in the final discussion.

The aim for this thesis is to provide the reader a sense of clarity about the former and current state of neuroaesthetics by highlighting important findings in the field, with specific focus of interest on the neural correlates of aesthetic appreciation of visual art. This will be achieved through collecting relevant literature in the field of neuroaesthetics with particular focus on the appreciation of visual art, meaning this is a literature review. Other fields such as artistic creativity, appreciation of music or dance will not be examined any deeper; unless considered relevant to the aim of this thesis. In order to capture the aim of the thesis, a brief philosophical background to aesthetics will be presented, followed by some insights on aesthetic appreciation from an evolutionary perspective. Thereafter, I will go through the role of aesthetic emotions in aesthetic experiences, as well as important theoretical frameworks and approaches in neuroaesthetics, and provide some basic knowledge of vision processing. Then there will be an overview of findings from some particularly outstanding studies on the neural correlates of aesthetic appreciation with focus on visual art; focusing on studies with only healthy subjects first and then studies with only non-healthy subjects. After that I will present some crucial conceptual, methodological and philosophical problems in neuroaesthetics, all of which will be examined in more detail in the final discussion. Lastly, some thoughts and improvements of the field will be presented in order to point neuroaesthetics in the right directions for future research.

General Observations on Art Theory

Many philosophers including, for example, Aristotle, Plato, Kant, Nietzsche, Heidegger and Schopenhauer, have all tried to determine the nature of aesthetic experiences and activities. Our understanding of aesthetic experiences started to be investigated greatly in the 18th century, when Western philosophers tried to shape a common notion of what art and beauty is, and how this notion should be considered (Sheppard, 1987). When considering aesthetic objects, it is indeed something about the beauty of such an object that seems timeless, and the feeling of experiencing an artwork or a natural scene can be most personal, differing among people with regards to their historical and cultural differences and the context the artwork is experienced in. Notwithstanding this, an aesthetic experience of a piece of art is not bound to one single perception of it, as one can easily see when presented with abstract paintings or artworks that have some degree of ambiguity in them (Zeki, 2004). As Heinrich (2013) has proposed, beauty of something can be defined as (but not be reduced to) the relationship of facts, ideas, lines, color combinations that make up a story or picture, a theory, or the very essence of truth. Beauty is in other words a concept that can vary depending on the context or the perception of it.

Sheppard (1987) discusses the variety of aesthetic experiences and that they are not only confined to sight but can be enjoyed in different forms such as listening to a waterfall, or smelling the scent of roses. These experiences can also be found when looking at natural objects, for instance the view of a beautiful mountain or the view of a sunrise. Humans are also very good at using imagination when exposed to an aesthetic experience. Examples of this could be things like seeing a dog-shaped cloud or hearing rhythmic patterns in dripping water. Although imagination plays a big role in (some) aesthetic experiences, not all of these experiences have to be shaped by elements of imagination but can also be enjoyed just as they are (Sheppard, 1987). Appreciation of formal arrangements is also aesthetically pleasing and plays an important role in our aesthetic response. For example, a well thought-out answer to a mathematical problem can be satisfying in an elegant way, or the balancing of furniture in an apartment may feel pleasing to the eye. Man-made objects or clusters of objects as well as arrangements can then be ascribed as beautiful, too (Sheppard, 1987). It is important to remember, however, that if one assigns a general feeling or mood to a specific view, then it is only because one has chosen to say that this particular scenery is ‘peaceful’ or ‘calming’ (perhaps when looking at a soothing garden, feeling calm and hearing the sounds of nature) and not because these objects that make up the view are naturally beautiful objects. Thus, objects that are considered beautiful are not autonomously beautiful, but they acquire these features through us (Sheppard, 1987). Perhaps it is also that it is not the objects themselves that are aesthetically pleasing, but rather we take on a special kind of aesthetic interest to these objects, something that we may choose to direct to anything we want, if we want to (Sheppard, 1987).

Aesthetic Appreciation and Evolutionary Theory

At first glance, one might believe that art-making and appreciation of art is a trait that is unique to humans. However, Heinrich (2013) has suggested that “art is not a uniquely human product, but a representation or an extension of the maker, as are the ornaments, displays and songs of a bird” (p. 743). Both humans and other animals have been observed producing aesthetic products and showing selective preferences over certain objects or ornamentations; a trait that is innate and species-specific. Birds, insects, great apes and many other animals have been observed making aesthetic judgments. Birds, for instance, are routinely observed making aesthetic decisions, like collecting feathers or shedding skins to decorate their nests, and also insects such as bumblebees show a distinct preference for blue flowers over other flowers (Heinrich, 2013). Allen (1880) also noted that certain animals are drawn to natural beauty, even though they are restricted in their preferences due to specific colors, forms and sounds made by their own species. However, these observations do not mean with certainty that these animals find some things 'beautiful' as they are strongly conditioned by food rewards unlike us humans (Heinrich, 2013), who may collect flowers because we simply see them as 'beautiful'.

The evolutionary history of aesthetic experiences has been examined for a long time and much puzzled the minds of early Darwinian thinkers, who attempted to account for the selective advantages of aesthetic production and appreciation (Nadal & Pearce, 2011). This branch of 'evolutionary aesthetics' mainly seeks out to understand the historical origins of aesthetic production and appreciation, i.e. why it exists at all and what the conditions are for it to still exist as a part of human behavior (Nadal & Pearce, 2011), as well as to understand the "sensory preferences in animals and humans that promote selective attention and positive emotional responses toward objects in the environment that lead to adaptive decision making and problem solving" (Brown & Dissanayake, 2009, p. 44). Since the theory of natural and sexual selection was proposed by Darwin (1991/1859), several theories have been proposed about why we appreciate art and how it fits into evolutionary theory (Nadal, Gomila & Gàlvez-Pol, 2013). Chatterjee (2014) has stated that there are typically two kinds of positions that evolutionary theoreticians adopt regarding this matter. One view is that art is an adaptation that gave our ancestors better advantages in survival and or replication, motivated by the observation that behaviors connected to art-making and appreciation are universal (Chatterjee, 2014). The main selective advantage from this capacity may likely have been to distinguish suitable environments from unsuitable environments (Clay, 1908; Nadal & Pearce, 2011).

Darwin (1991/1859) suggested that music might have evolved in support of mate choice through sexual selection. This suggestion may indicate that humans with artistic abilities pay high costs for their rare and difficult skills, which might serve as advantageous in terms of reproduction and survival, signaling honest qualities such as high intelligence, creativity, good learning abilities and health, all of which are positive characteristics (Nadal & Pearce, 2011). Grammer, Fink, Møller and Thornhill (2003) noted that the obsession of beautiful things in humans is similar to obsessions that are present in other animals. This may reflect the influence of human mate criteria on our perception of beauty and the shaping of it, across human evolutionary history (Grammer et al., 2003). The ability to distinguish fine art from its counterpoint may then be an evolutionary trait passed on from our early ancestors, who possessed this ability in a more rudimentary form. For example, great apes and humans share preferences for curved contours over sharp contours, which might have influenced other visual preferences as well, such as art (Munar, Gómez-Puerto, Call & Nadal, 2015). Perhaps these types of preferences for certain environments can then be explained as beneficial for our survival, passed on to us from our ancestors.

The other view, motivated by the observation that art is culturally contingent and varies highly in different aspects, sees art as an exaptation or an epiphenomenon (Chatterjee, 2014). Exaptations are properties of an organism which evolved to perform one function, but are forced to perform another function because of selective pressures (De Sousa, 2004). De Sousa (2004) argues that most adaptations in fact are exaptations and refers to the innateness of art; describing that some things that are innate are not universal and some things that are universal are not innate. He further claims that art is the result of our brains wanting to understand our environments, since it is beneficial for our survival, and that the feelings of pleasure one feels when understanding the environment act as motivators, and therefore art can be seen as an exaptation of our desire to interpret external stimuli (De Sousa, 2004).

These emotions one has when engaging in aesthetic activities, possibly acting as motivators for survival and reproduction, are of interest in order to understand aesthetic appreciation. With this in mind, I shall now go through what aesthetic emotions might mean to aesthetic experiences and how they relate to regular everyday feelings that are devoid of aesthetic contexts.

Aesthetic Emotions in a Biological Context

Presumably, the most immediate emotional responses to an aesthetic object, whether it be a painting, sculpture or craft, would be the kinds of emotions that are purely reflexive and autonomous; producing very small and quick changes in skin conductance, heart rate and pupil dilation, which are reflections of our parasympathetic and sympathetic neuronal systems (Chatterjee, 2014). Nonetheless, viewing an artwork always begins with molecular events occurring in the retina, which sends these signals through the thalamus and the cortex, where the signals then are analyzed in terms of color, form, depth, spatial organization and so on (Changeux, 2012). Suppose a person is viewing a painting containing forms, lines and colors of various fashion. Neurons that are selective to those exact features will respond accordingly, with color being processed in one area; forms and lines of different orientations in another; movement and depth and the discrimination of figure from background in another area, and other features (Changeux, 2012; Zeki, 2004; Zeki & Bartels, 1999). The processing time of these various visual features has been shown to be differing in time span, with for example color seeming to precede motion by around 80 milliseconds (Zeki & Moutossis, 1997). Although viewing artworks typically involve the same areas of the brain, different artists may use different techniques to convey specific emotions to the observer**.** It might be safe to say that abstract or indeterminate art don’t seem to convey the same types of emotions that one might experience when looking at representational works, since it may be harder to be ‘emotionally struck’ by an abstract painting with only variations of colors and no depicted face expressions, body language, landscapes or anything that can portray grand human emotions such as beauty, tragedy, moral, political values and so on. Thus, it is this ability of conveying strong human emotions that artists have used successfully for ages and continue to do today in order to evoke strong emotional reactions or pleasures, as well as non-pleasures or disgust. But how exactly can we understand these aesthetic emotions in relation to ‘regular’ emotions?

Chatterjee (2014) discusses how these two types of emotions can be separated by addressing the importance of contextual presentation. For example, reading a frightful book does not compel one to rush out in panic and fear, but because of the specific presentation of the fearful stimulus and the context of it, the emotion is transformed into an aesthetic emotion (Chatterjee, 2014). As Kant’s (1790/1911) notion about ‘disinterested interest’ goes about, being emotionally absorbed and at the same time disinterested perhaps reflects a lack of action since the aesthetic emotion does not necessarily make the viewer approach or avoid something. Going further down this path, as identified by Berridge, Robinson and Alridge (2009) there seems to be two reward systems for ‘liking’ versus ‘wanting’. The ‘liking’ is mediated by cannabinoid and opioid neurochemical systems, referred to as a direct experience of pleasure, and the ‘wanting’ is mediated by dopaminergic neurochemical systems, referring to the desire of an object and the action taken in order to satisfy that desire (Berridge et al. 2009). Experiencing the ‘liking’ without the ‘wanting’ might then be the biological equivalent of Kant’s ‘disinterested interest’, describing how one can like something without making an active pursuit to it. However, the claim by Chatterjee (2014) is not that art itself can generate emotions which in their turn incite actions, but rather that emotions that incite actions are not considered aesthetic emotions. This is interesting to reflect on because one might ask if an aesthetic emotion is really bound to not incite actions by all means. If an artwork incites an action, it should not be considered an aesthetic emotion anymore; but some kind of emotion will still be *felt*, regardless of its nature and how or if we attempt to pursue that emotion. The question here that one might be tempted to infer from Chatterjee's (2014) statement may therefore be whether or not art can still be considered as art if it does incite actions. Unfortunately this discussion is, although interesting, outside the scope of this thesis.

The issue of separating an aesthetic emotion from other emotions may seem like more of a matter of conceptual finesse than of conducting ingenious experimental designs. Perhaps this is due to the fact that there is not a dedicated aesthetic module in the brain that handles all aesthetic experiences (Chatterjee, 2014), but rather that these experiences emerge from sensory-motor, emotion-valuation and knowledge-meaning systems that are interacting with each other (Vartanian & Goel, 2004; Nadal & Pearce, 2011; Vartanian & Skov, 2014). Great works of art are known to affect and remain deeply in the observer's mind, sometimes lasting in short durations and sometimes for a whole lifetime. The problem of how emotional responses to art can be measured in terms of neural connectivity may perhaps be solved through the use of clear, methodological frameworks. Such frameworks or models have been suggested but none have been exclusively prioritized in neuroaesthetics (Zaidel et al., 2013). Therefore, the next part will be about some chosen proposed models of aesthetic appreciation; what their respective approaches to experimental aesthetics are and what they have meant to the field of neuroaesthetics.

Theoretical Frameworks within Neuroaesthetics

Empirical approaches to art have been much influenced by formalist views on art and aesthetics (Bell, 1914). One aspect of the empirical approach to neuroaesthetics has been to seek to develop and test general hypotheses that can predict responses in individuals, across different contexts and experiences, whereas another aspect has focused on the humanist approach which has been the most common one due to the interest of subjectivity, with particular aim on the stylistic, iconographic and formal details of aesthetic experiences (Nadal & Pearce, 2011). Since the early 21st century, there have been technological advances in measuring and quantifying data which have made it possible for art and aesthetics to finally be examined empirically in the lab environment. Neuroscientists are now able to use different measuring techniques and sophisticated computer programs to explore the conceptual and neural foundations of aesthetic appreciation and production, as well as artistic creativity (Leder & Nadal, 2014). Despite these progresses, neuroaesthetics still lack a unified theoretical framework (Nadal, Munar, Àngel Cápo, Roselló & Cela-Conde, 2008), although some attempts have been proposed in the past. Fechner (1876) is generally considered to be the first who conducted studies on empirical aesthetics, and who, along with Wundt, established the foundation of scientific experimental psychology through their respective work (Nadal & Pearce, 2011). Allen (1880) and Darwin (1991/1859) advocated the roles of sexual selection and survival in the origin and evolution of aesthetic experiences, as well as Clay (1908), who argued that aesthetic experiences are essentially built from our abilities to assess the suitability of environments in terms of potential resources and dangers, which all ultimately affect the ability to survive. Since then, psychological approaches such as Gestalt psychology have treated human experiences as a holistic field where parts interact with each other dynamically and are influenced by the whole field (Nadal et al., 2013). According to Gestalt psychology, the perception and binding of objects and scenes are therefore an emergent process which is built on the constitution of elements that make up a whole experience (Nadal et al., 2013). Along with the onset of the behaviorist era aesthetics suddenly became a non-central topic of interest, since subjective experiences were of no interest to behaviorists (Leder & Nadal, 2014). During the 1960's and 1970's (Nadal et al., 2013), aesthetics became interesting again when Berlyne (1974) proposed his 'psychobiological aesthetics' as a psychobiological framework of approaching experimental aesthetics, which focused on arousal as being the main drive for curiosity and exploration, associated with hedonic pleasure (Berlyne, 1974; see also Leder & Nadal, 2014). This framework focused on the explanation of preferences of people and animals for certain kinds of stimuli and later formed the starting point of contemporary experimental aesthetics (Nadal et al., 2013). Berlyne (1974) suggested that the interest and preference of a given work depends on how complex the stimulus appears to the person, whether the stimulus is of visual or musical nature. After Berlyne (1974), other frameworks or models with more neuroscientific focus have been proposed. Leder, Belke, Oeberst and Augustin (2004) proposed a model of aesthetic appreciation which states that our experience and aesthetic judgment of an artwork goes through several stages of affective evaluation, aiming to describe the psychological mechanisms that are supposedly involved in the aesthetic appreciation of art. Our aesthetic judgments are, according to this model, a result of the evaluation of the cognitive mastering stage while our aesthetic emotions are labeled as an emotional reaction that is considered a byproduct of the processing stages in these models (Leder et al., 2004). This framework was influenced by an early methodological approach to the experimentation of art and aesthetics by Fechner (1876) and was recently reviewed by Leder and Nadal (2014), where the state of this model was reviewed and accounted for. Another theoretical framework is the 'aesthetic triad' proposal by Chatterjee and Vartanian (2014), which describes that an aesthetic experience arises due to interactions between sensory-motor, emotional-valuation and meaning-knowledge systems. It is because of this complex interplay between these neural systems that one can have a *sensation* of something that is also semantically *meaningful* to him or her (Chatterjee & Vartanian, 2014). These psychological mechanisms enable us to evaluate the experience and to be affectively absorbed by it, which is meaningful both socially and individually (Leder & Nadal, 2014).

Processing Stages of Visual Attributes

Functional Specialization in Vision

From the 60's up to the late 90's, Semir Zeki conducted extensive research on the visual processing systems, essentially discovering the functionally specialized areas of visionary attributes. As previously found in the macaque monkey, it is today widely agreed that the human prestriate cortex also consists of several functionally specialized areas of vision processing that are specialized in different attributes of vision, e.g. area V4 for color, V5 for motion (Zeki et al., 1991; Zeki, 2004). Zeki's work on mapping out the visual systems also binds together with the study of consciousness, as his micro-consciousness theory suggests that activity at the different stages of visual processing creates anatomically separate, functionally specialized micro-consciousness correlates that are distributed in the brain (Zeki, 2004; Zeki & Bartels, 1999). Each micro-conscious correlate is a direct reflection of the activity that is occurring at a specific node or visual processing area (Zeki & Bartels, 1999). Signals from the retina first reaches the primary visual cortex (V1) through the thalamus and then gets further transmitted through surrounding areas (V2) and specialized compartments within these areas. The signals from V1 and V2 project to V4 (color) and V5 (motion) and their respective sub-compartments and since the latter areas do not need further processing they are considered as essential nodes, e.g. the signals become conscious and explicit there (Zeki, 2004). This means that if area V4 and V5 would be destroyed, then the ability to perceive color and motion would now be directly influenced by the physiological capacities of the neurons in areas V1 and V2 since forwarding these signals would no longer be possible (Zeki, 2004). However, it is known that these specialized areas of the visual cortex are also acting as both transmitters and receivers of signals, as they are mutually interconnected and can thus be assumed to communicate with each other without the need of a centralized unit handling all communication for visual information (Douchová & Nešetřil, 2010).

Color Processing

It is known that color processing occurs primarily in the compartments of area V4 in the occipital cortex (Zeki, 2004). Zeki and Moutossis (1997) conducted a study where the aim was to reveal the temporal hierarchy in visual perceptive systems, focusing on the temporal differences in processing color and motion, respectively. A Mondrian figure was used (an abstract multi-colored scene with no clear recognizable objects) with red and green squares moving up and down against the Mondrian background, shifting from red to green and vice versa with the change in direction of motion (Zeki & Moutossis, 1997). Their results were, as before, still consistent with the fact that color is perceived before motion, by about 80 milliseconds. The processing of color has been further investigated by Zeki and Marini (1998), where it was observed that subjects who looked at normally colored objects of a Mondrian scene had their anterior parts of the fusiform gyrus, the hippocampus and the ventrolateral frontal cortex activated. In contrast, abnormally colored objects activated the dorsolateral frontal cortex, suggesting that there are different cortical stages of color processing in the brain (Zeki & Marini, 1998).

Ambiguity

Understanding how ambiguity is dealt with in the brain is important to the study of brain mechanisms of aesthetic judgment (Goldberg, Funk & Podell, 2012) and also in order to gain knowledge of interactions between cerebral areas. There is a wide range of artworks and paintings that all share the feature of ambiguity in them, such as the well-known 'wife/mother-in-law', Giuseppe Arcimboldo's 'Vertumnus' and many other works of art. Paintings that are open to multiple interpretations (all of them equal in validity) can be interpreted in different ways. However, the brain can only answer to one plausible interpretation at a time since objects that are available to two or more interpretations serve equal validity (Zeki, 2004). It has been argued (Changeux, 2012) that what is seen as a part of an ambiguous figure is what has currently gained access to a ‘global neuronal workspace’. The thought of a global workspace serves as a useful metaphor in explaining how the brain ‘chooses’ some interpretations over others, or put differently; why some interpretations are made available to the perceiver (c.f. the ‘Cartesian theatre’). Conscious access through a globally distributed network is an endogenous process which makes both external and internal content available to several brain systems, allowing for an aesthetic experience to take place within such a network (Changeux, 2011; Changeux, 2012).

Neural Correlates of Aesthetic Appreciation

It has been argued (Changeux, 2012) that appreciation of art is first and foremost a product of neuronal signaling and physio-chemical reactions in the brain, and that it can also be shaped by interactions with our environment, such as social and cultural factors, due to the epigenetically evolved brain that we humans possess. The human brain has not appeared very suddenly but has evolved and developed from our early ancestors, with oral language, art and books transmitting knowledge and contributing to the growing and passing of cultures, and thus the passing of concepts such as art. Despite the very long time that the human brain has had to develop the ability to appreciate art, as well as produce it, the very appreciation of art only happens in a very short amount of time, in the hundreds of milliseconds (Changeux, 2012). According to Nadal and Pearce (2011) the aesthetic appreciation of visual art, dance and music all involves at least three different kinds of neural activity that can be measured. These are: (i) Low-level cortical sensory processing; (ii) top-down processing and the activation of cortical areas involved in evaluative judgment; and (iii) the activation of the reward circuit, including both cortical and sub-cortical regions (Nadal & Pearce, 2011). In several of the studies that will follow in this part of the thesis, these types of neural activation can be found in most of them. I will now go through some of the more important studies that have contributed to an increased understanding of the neural underpinnings of appreciating art. The starting point will be on different aspects of aesthetic appreciation of art in healthy subjects, and then I will move on to describe some common visual and cognitive deficits and in what ways they affect the aesthetic appreciation of art in non-healthy subjects.

Aesthetic Appreciation in Healthy Subjects

Viewing paintings. In 2004, Vartanian and Goel conducted one of the first neuroscientific studies on aesthetic appreciation. The participants consisted of twelve right-handed female subjects with no history of neurological or psychiatric disorders, and were asked to rate paintings from three categories based on their aesthetic preference. The categories were: original paintings (pictures of original paintings), altered (same pictures but with one or more objects moved or changed in the painting) and filtered (same paintings but with a filter put over the painting). Activity was measured via fMRI and the results demonstrated that activation in the right caudate nucleus decreased in response to decreasing preference, and that activation in bilateral occipital gyri, bilateral fusiform gyri and the left cingulate sulcus increased in response to increasing preference (Vartanian & Goel, 2004). These findings suggest that aesthetic preference for paintings is related specifically to structures involved with the evaluation of reward-based stimuli that vary in emotional valence, and could also imply increased visual attention in response to higher preference rates (Vartanian & Goel, 2004). The importance of reward-related structures has been further implied by Vessel et al. (2009) where it was concluded that the strength of an aesthetic experience correlates with specific activity in the prefrontal and subcortical reward circuitry, which continues to support the importance of cognitive and reward-based systems in aesthetic experiences.

Ishizu and Zeki (2013) conducted a study where twenty-one normal subjects participated (11 males and 10 females, all untrained artists or musicians except for one male, mean age 28.8 years). Their brain activities were recorded while judging the beauty and brightness of paintings that were presented simultaneously to them, by means of fMRI. Areas that showed activation were the medial and lateral subdivisions of the orbitofrontal cortex (OFC; moral judgment, cognitive control), as well as subcortical areas involved in affective motor planning, such as the global pallidus, putamen-claustrum, amygdala and the cerebellar vermis. Furthermore the premotor, motor and supplementary motor areas including the anterior insula and the dorsolateral prefrontal cortex were also activated during judgment of both beauty and brightness (Ishizu & Zeki, 2013). These findings suggest several things: that there is a functional specialization for aesthetic judgment, that the systems activated show correlation in activity with polar experience (e.g. love-hate, beauty-ugliness), and that there also exists a functional specialization in the motor pathways for engaging aesthetic judgments (Ishizu & Zeki, 2013).

Vartanian & Skov (2014) conducted a quantitative meta-analysis of fifteen experiments measuring the neural correlates of viewing paintings under varying cognitive demands. By means of the collected evidence from the fifteen experiments, they concluded that paintings correlated with activation in the occipital lobes (the visual system), fusiform gyrus and parahippocampal gyrus (structures related to object and scene perception) and the anterior insula (a key structure involved in the experience of emotions) (Vartanian & Skov, 2014). Two hypotheses were made about what structures would be activated when viewing paintings. The first hypothesis stated that viewing paintings should activate areas in the visual cortex; including the lingual gyrus, middle occipital gyrus and the fusiform gyrus, whilst the second hypothesis stated that areas involved in place and object detection should be activated upon viewing paintings (Vartanian & Skov, 2014). The first hypothesis was confirmed since the processing of shapes, colors and orientation as well as grouping of visual features occurs in the visual cortex since this part of the brain is necessary for the visual analysis of a painting. The second hypothesis was also confirmed since it was observed that the fusiform gyrus and the parahippocampal gyrus were activated, areas which are known for their roles in perception and recognition of objects, as well as the perception and recognition of places, respectively (Vartanian & Skov, 2014). The activation of these specific areas likely arises partly due to the object detection that is made when looking upon pictures with rich content and partly due to viewing natural scenes, such as landscapes. Furthermore, the inferior temporal cortex was also activated; known for its well-known role in the representation of color and form, as well as the precuneus; most likely because of its contribution to visuo-spatial exploration of pictorial stimuli (Vartanian & Skov, 2014). It might sound trivial to base these two hypotheses on the activation of visual systems and object/place perception systems, since these areas are always activated in healthy subjects when viewing any visual content. However, the data collected from this study still serve to support the importance of these particular neural structures in the appreciation of visual stimuli, such as paintings (Vartanian & Skov, 2014).

Viewing sculptures. Di Dio, Macaluso and Rizzolatti (2007) used fMRI to investigate whether or not there is an objective basis of aesthetic appreciation in human subjects that were naïve to art criticism. The subjects consisted of fourteen healthy right-handed males and females (8 males; 6 females) and all were educated undergraduate or graduate students with no experience in art theory. By manipulating the independent variable (proportion), two groups of images were produced that contained original images of famous sculptures and modified versions of the same sculptures, where the trunk:legs relation were modified so that in one image the sculpture had longer legs and shorter trunk, and vice versa (Di Dio et al., 2007). The two groups of stimuli were presented in three conditions and these were observation, proportion judgment and aesthetic judgment. In the observation condition (O), the subjects were asked to look at the images with the same mind-set as if they saw the images in a museum and make an indication of whether or not they were paying attention to the image. In the other two conditions, they were asked to make either proportional (PJ) or aesthetic (AJ) judgments about the sculptures. These tasks were done by pressing one button for ‘yes’ and one button for ‘no’. In other words, participants were required to make a response in all the three conditions, stating whether or not they paid attention to the presented image (O), aesthetically liked the presented image (AJ) or thought the presented image was proportionate (PJ). In the O condition (when the participants observed the original unmodified images), a strong activation was noted in the right insula as well as activation in the lateral occipital gyrus, prefrontal areas and precuneus, relative to the modified images (Di Dio et al., 2007). In the AJ condition (when participants made aesthetic judgments on the same images), the right amygdala was selectively activated when the participants judged the sculpture as beautiful, as relative to the ones that were judged as ugly (Di Dio et al., 2007). These results are in line with previous findings which highlight the involvement of the amygdala and insula upon making aesthetic judgments on visual art (Adolphs & Tranel, 1999; Ishizu & Zeki, 2013; Vartanian & Skov, 2014) as well as music (Gosselin, Peretz, Johnson & Adolphs, 2007; Griffiths et al., 2004). In the light of these results, Di Dio et al. (2007) concluded that objective beauty as such lies in the activation of the insula and subjective beauty in the amygdala, as the sense of beauty seems to be mediated by these two separate processes. The results also support the importance of the prefrontal areas when making judgments of aesthetic stimuli, as have been accounted for in both past and recent studies (e.g. Cela-Conde et al., 2004; Kawabata & Zeki, 2004; Changeux, 2012; Ishizu & Zeki, 2013; Jacobsen, Schubotz, Höfel & von Cramon, 2006).

Preferences for scenes and landscapes. It has been demonstrated that viewing pictures of pleasurable places or scenes activates the parahippocampal place area and the ventral striatum (Yue, Vessel & Biederman, 2007), suggesting the engagement of the reward system (Vartanian & Skov, 2014), as well as the fusiform gyrus (Vartanian & Goel, 2004). Yue et al. (2007) conducted a study where fourteen graduate or undergraduate students participated, with data collected from only twelve participants since two were excluded due to excessive head movement. The participants were shown images of different types of scenes and landscapes, and it was found that viewing highly preferred scenes such as natural scenes, city streets and rooms was associated with greater BOLD-signals (blood- oxygen level dependent) in the right parahippocampal cortex, compared with scenes that were rated as less preferred (as rated by the participants). The parahippocampal place area is highly dense in cortical μ-opioid receptors, which are suggested to subserve visual recognition (Yue et al., 2007). These receptors are found along the ventral visual pathway where the receptors are sparse in the first stages of visual information processing (e.g. V1 and V2) and then gradually increase in density when moving up the pathway, where the maximum density of these receptors are found in the parahippocampal gyrus (Yue et al., 2007). Furthermore, Vessel and Rubin (2010) found that individual observations for abstract and real-world images yielded consistent visual preferences, suggesting that the typical driving force of visual preferences is the semantic content of the image. The high agreement of preferences for real-world scenes across observers appears to be influenced by the observers' shared semantic interpretations and by the fact that the effect of these shared interpretations can be reduced due to the nature of the context (Vessel & Rubin, 2010). Low agreement across observers, on the other hand, may simply indicate that people like different paintings, as assessed by behavioral results (Vessel et al., 2009).

Judgment and appreciation of beauty and ugliness. Kawabata and Zeki (2004) conducted an experimental study where the goal was to reveal whether or not there are certain brain areas that are specifically activated when subjects view paintings that they consider to be beautiful or ugly, by means of fMRI. Five female, healthy, right-handed subjects were presented to four categories (portrait, landscape, still life and abstract composition) which altogether consisted of a large number of paintings. The paintings were then classified into beautiful, ugly or neutral by the subjects. The subjects later viewed the same paintings again while in the scanner. The results showed that the OFC was activated differentially when the subjects perceived beautiful and ugly stimuli, regardless of the category of the painting, and that the perception of paintings from different categories were associated with specialized areas in the visual brain (Kawabata & Zeki, 2004). An interesting observation was that the motor-cortex was activated when viewing paintings, with ugly stimulus mobilizing the motor system more than the beautiful stimulus did (Kawabata & Zeki, 2004); perhaps suggesting that viewing ugly or beautiful stimuli mobilizes the motor system in order to make an action or response to the beautiful stimulus, or to avoid the ugly stimulus (Ishizu & Zeki, 2013; Kawabata & Zeki, 2004), or potentially harmful objects (Munar et al., 2015). The preference of ‘softer’ objects over ‘sharper’ ones was recently discussed in a study where it was observed that great apes and humans both seem to share a visual preference for curved contours over sharp contours; something that have been suggested as an adaptive trait evolved specifically for the avoidance of potentially dangerous objects (Munar et al., 2015). This may suggest that the inherited preference for curved contours in humans could date back to earlier primates’ visual preferences and that during this process the preferences for other visual features may have been influenced as well, such as appreciation for art (Munar et al., 2015).

Around the same time as the previously mentioned study by Kawabata and Zeki (2004), Cela-Conde et al. (2004) conducted a study where the prefrontal cortex was highlighted as especially important in terms of neural activity when participants qualified some objects as ‘beautiful’. The goal in this study was to investigate whether or not the prefrontal areas are activated when a person perceives art as beautiful. In order to examine this, eight female subjects with an average age of 20 years and no previous art training were presented with stimuli consisting of natural and artistic colored pictures, divided into five groups of different art categories. In these five groups were (i) 40 pictures of abstract art; (ii) 40 pictures of classic art; (iii) 40 pictures of Impressionist art; (iv) 40 pictures of Post-Impressionist art and (v) 160 photographs of different landscapes, urban scenes and artifacts, among some. Their brains were scanned by means of MEG (magnetoencephalography) and the results showed that the left prefrontal dorsolateral cortex (PDC) was activated when the subjects perceived beautiful stimuli, regardless whether the stimuli was natural or artistic (Cela-Conde et al., 2004). The latency of the activation took place at around 400 – 1000 ms, which is crucial because it corresponds with previous notions that different visual attributes are perceived at different times (Cela-Conde et al., 2004), and that they are also processed at different sites in the brain (Zeki & Moutossis, 1997). The results demonstrated that cortical activity in the PDC corresponds with aesthetic perception, and also that the activity is greater in the left hemisphere when a person makes an aesthetic judgment (Cela-Conde et al., 2004). This might be connected to language, since the processing of language also is localized specifically in the left hemisphere (Zaidel, 2010).

Gender-related differences. Our knowledge about the neural correlates of beauty is slowly growing, but still very little is known about gender-related differences in aesthetic appreciation. Cela-Conde et al. (2009) performed an experiment to reveal whether or not such differences may exist when it comes to aesthetic appreciation, and to what extent gender might influence how beauty is rated. Ten males and ten females were presented with natural and artistic stimuli and were asked to rate how beautiful they found each. By means of MEG, it was found that the parietal regions were activated while subjects viewed stimuli as ‘beautiful’, with women showing bilateral activity and men lateralized activity in the right hemisphere (Cela-Conde et al., 2009). Moreover, the activity in the parietal regions was also reported as greater when participants rated the stimuli as beautiful, rather than not beautiful (Cela-Conde et al., 2009). The authors concluded that the differences between genders that were found here were due to evolutionary processes that followed the splitting of chimpanzee and human lineages, suggesting that men and women form different strategies in assessing aesthetic preferences, which might be a reflection of how our hunter-gatherer hominin ancestors divided labor between males and females. Activity in the parietal regions has previously been associated with spatial ability and mental rotation (Koscik, O'Leary, Moser, Andreasen & Nopoulos, 2009). According to Cela-Conde et al. (2009), these mental features are crucial for the human appreciation of beauty and are also considered as primary components of such appreciation in both sexes.

Facial attractiveness and symmetry. O'Doherty et al. (2003) measured facial attractiveness response in thirteen healthy males and twelve healthy females by means of fMRI. It was found that activation in medial OFC was revealed when participants viewed an attractive face with neutral face expression. The activation in that area was enhanced when the participants viewed the same attractive face but with a smiling face expression, suggesting that smiling enhances the reward value as indexed by medial orbitofrontal activity (O'Doherty et al., 2003). Moreover, as found by Ishai (2007) there seems to be a correlation between strong activation in the OFC and higher sexual preference for faces. Forty right-handed and normal participants (10 heterosexual women, 10 heterosexual men, 10 homosexual women, 10 homosexual men) rated gray scale pictures of 100 women and 100 men on the basis of facial attractiveness and pressed one of three buttons to indicate whether each face was perceived as Attractive, Neutral or Unattractive. Their brain activity was measured by means of fMRI and the results showed that preferences for beautifully perceived faces are represented by activity in the OFC across gender and different sexualities, which was also found to be irrespective of reproductive fitness since the subjects consisted of both heteroand homosexual men and women (Ishai, 2007). This is in contrast to the view that the perception of attractiveness in humans is sex-specific since both genders can have different mate preferences (Grammer et al., 2003).

Both physical symmetry and physical attractiveness have now been widely investigated in relation to facial features in humans, but also in relation to bodily features of other animals (Heinrich, 2013). Samuels, Butterworth, Roberts, Grauper and Hole (1994) investigated how visual preferences of attractiveness varied in human babies with relation to vertical symmetry. The babies looked longer at normal and chimeric attractive faces than at normal and chimeric unattractive faces, with infants as young as 4 months old showing distinct preference for the attractive faces (Samuels et al., 1994). The evidence gathered here led to the conclusion that infants are hardwired to prefer attractive faces (as rated by adults) over unattractive faces and also that the attractiveness of a face is not only determined by the vertical symmetry around the vertical midline (Samuels et al., 1994). In another study by Jacobsen et al. (2006), participants were asked to make aesthetic judgments based on the perceived beauty and symmetry of geometric shapes. The participants were fifteen right-handed, healthy volunteers (6 males, 9 females), none with any professional training in the fine arts and all with normal or corrected-to normal vision. The stimulus material was presented as novel, abstract graphic patterns and participants were instructed to make aesthetic evaluations, i.e. state if it was beautiful or not, and descriptive symmetry judgments, i.e. if it was symmetrical or not, on the same stimulus. These kinds of graphic patterns were used in order to minimize memory-related processes and attitudes that might act as confounding variables, by testing the effects of the stimulus symmetry and complexity on the participants (Jacobsen et al., 2006). The employment of complex symmetrical stimuli was used for comparison, since judgments of beauty often involve the judgment of stimulus symmetry (Jacobsen et al., 2006). The aesthetic judgments showed specific activations in the temporo-parietal junction, left temporal pole, posterior cingulate, bilateral prefrontal and frontomedian cortex, as assessed by means of fMRI (Jacobsen et al., 2006). The frontomedian cortex, as well as the intraparietal sulcus, showed enhanced blood-oxygen-level (BOLD) signals when participants judged something to be beautiful, and moreover, the stimulus complexity was shown to cause differential effects on the two judgment types (Jacobsen et al., 2006). These findings indicate that aesthetic judgment and judgment of beauty triggers a network in the brain which is involved in evaluative judgments of social and moral cues, as was assessed by fMRI results and behavioral data (Jacobsen et al., 2006).

Taking the abovementioned results into account, they seem to suggest highly complex patterns of brain activity in supposedly different neural networks and pathways (O'Doherty et al., 2003; Samuels et al., 1994). The specific preference of some aesthetic objects over others does not only concern visual art, but the same principles can be applied to other types of perceived objects such as music, dance and poetry (Brown, Gao, Tisdelle, Eickhoff & Liotti, 2011). Now that I have gone through the neural correlates of aesthetic appreciation in healthy subjects put under various types of cognitive demand, it is time to look at how damages to the cognitive and emotional functions of the brain affect the way we appreciate different aspects of art.

Aesthetic Appreciation in Non-Healthy Subjects

Amygdala damage. It is known that the amygdala guides specific preferences for visual stimuli that are normally considered aversive, and it has also shown to be involved in the processing of emotional and social stimuli (Adolphs & Tranel, 1999). In a study where visual preferences for different visual content were compared between two groups of healthy subjects and subjects with bilateral amygdala damage, Adolphs and Tranel (1999) revealed that there were consistent differences in visual preferences. The subjects with amygdala damages showed a positive bias for simple figures, patterns and geometrical shapes, as the impairment resulted in an appeared higher liking for visual content that are normally liked the least (Adolphs & Tranel, 1999). It has also been assessed through another study by Gosselin et al. (2007) that the amygdala also plays an important role in the recognition of fear from music, where rare female subject S.M. (whom suffered from relatively restricted bilateral damage to the amygdala) identified happy music as normal and scary music as less fearful than controls. Although she recognized happy music as much as normal as the controls did, she reported that peaceful music was less relaxing compared with how the controls perceived it. Since other features were spared from the impairment, these findings serve to suggest that the amygdala indeed plays a key role in determining the social and emotional value of auditory and visual aesthetic content (Adolphs & Tranel, 1999) as well as the recognition of fearful or sad stimuli in music (Gosselin et al, 2007). Therefore, the amygdala appears as necessary in the emotional processing of music, which can be further suggested to apply in much the same way as when we look at visual art (Changeux, 2012; Ishizu & Zeki, 2013).

The effect of strokes on musical enjoyment. Griffiths et al. (2004) describe a case where a male patient suffered a stroke in the left insula (extending into the left frontal cortex and amygdala), after which he was found to be emotionally unaffected by music (also known as 'musical anhedonia'). Since he could still enjoy other types of activities, the researchers behind the study concluded that there must be separate neural networks that are responsible for the emotional processing of music, which then rests on functionally and anatomically different neural networks (Griffiths et al., 2004). The insula in particular seems to be a crucial piece in the emotional response to music, which likely functions in much the same way as in the emotional response to visual art (e.g. Griffiths et al., 2004; Ishizu & Zeki, 2013; Vartanian & Skov, 2014). In a similar case study Satoh et al. (2011) investigated a patient who, after experiencing an infarction, found himself unable to experience any emotions when listening to music. As in the study by Griffiths et al. (2004), the patient here had also been able to feel emotions when listening to music prior to the lesion. A magnetic resonance imaging (MRI) was conducted where the infarction was revealed in the right inferior parietal lobule and it was concluded that the right parietal lobe seems to be involved in the emotional experience one has when listening to music (Satoh et al., 2011). This conclusion was based on the fact that the patient's other musical and neuropsychological skills were unharmed after the onset of the infarction, suggesting that these abilities get processed through other neural networks (Satoh et al., 2011). As mentioned previously in this thesis, the parietal lobe in males have been shown to display specific activation when a painting is viewed as beautiful (Cela-Conde et al., 2009), which can be attributed to the findings from the study by Satoh et al. (2011), further suggesting that the emotional experience of viewing paintings are lateralized to the right hemisphere in males, and that they are necessary for the ability to experience emotions when engaging in art.

Stability of visual art preference in Alzheimer's patients. It has been found that patients with Alzheimer's disease (AD) show stability in art preferences over time, in more or less the same degree as healthy subjects (Halpern, Ly, Elkin-Frankston & O'Connor, 2008). Halpern et al. (2008) conducted two studies where art preference was compared between one group of Alzheimer's patients and one group of age-matched control participants. It was observed that both the control group and the AD group had about the same stability in terms of art preference as measured over two weeks, even though the AD patients had no explicit memory of having them expressed that they liked one painting more than the other; suggesting that art preferences can be maintained in spite of cognitive decline (Halpern et al., 2008).

Post-surgical changes in aesthetic taste. Sellal et al. (2003) describe an eighteen year old epileptic patient who had experienced brief losses of consciousness followed by a mild anomia, whereby the patient later underwent temporal lobe resection in order to cure the epileptic seizures. This was done by removing the anterior pole, T2, T3, T4 and T5. After the surgical resection of the small neocortical temporal area was performed, the patient found himself to have changed his taste in music, art and literature (Sellal et al., 2003). The patient now had trouble listening to rock music which he previously enjoyed, and had also stopped enjoying reading sci-fi novels, moving towards more Kafkian-inspired novels (Cela-Conde et al., 2011), while also liking realistic paintings more, noticing more details in them and expressing the appreciation of these small, previously unnoticed details (Sellal et al., 2003). This case is interesting due to the fact that the areas that were surgically removed roughly corresponds to the areas which are typically degenerated in fronto-temporal dementia; a cognitive deficit which has been shown to, among other things, drastically affect the musical preferences of patients suffering from this disease, making them listen compulsively to new music for long sessions (Cela-Conde et al., 2011). Although the surgical procedure cured the man of his epilepsy, it clearly changed his aesthetic taste in numerous categories while leaving his personality and taste in other things untouched, such as preference for food and faces (Sellal et al., 2003). However, taste preferences for more basal needs such as food are to a large extent innate and are therefore not so easily disrupted (Heinrich, 2013).

Discussion

The aim for this thesis has been to present evidence from both older and newer studies in the field of neuroaesthetics, particularly focusing on the aesthetic appreciation of visual art. Since aesthetic appreciation of art is a phenomenon which seems to be highly complex and consist of different networks interacting with each other in the brain, it is therefore also complex to draw conclusions and connections between the evidence. However, when looking at all the gathered evidence from the studies featured here, a number of patterns start to emerge. As seen in this thesis, several studies have showed the importance of the prefrontal areas (e.g. Di Dio et al., 2007; Jacobsen et al., 2006), in particular the dorsolateral prefrontal cortex (e.g. Cela-Conde et al., 2004; Ishizu & Zeki, 2013), and the OFC (e.g. Ishai, 2007; Ishizu & Zeki, 2013; Kawabata & Zeki, 2004; O'Doherty et al., 2003) in making aesthetic judgments. Both the medial OFC (Ishizu & Zeki, 2013; O'Doherty et al., 2003) as well as the lateral OFC (Ishizu & Zeki, 2013) have shown to be activated when subjects regard something as beautiful. This is most likely due to the fact that the prefrontal cortex is involved with cognitive demands such as decision-making, which can be further validated through the results of other studies (e.g. Cela-Conde et al., 2004; Di Dio et al., 2007; Ishizu & Zeki, 2013; Jacobsen et al., 2006, Vessel et al., 2009). These findings strengthen the idea that the prefrontal areas, especially the OFC, are necessary in order to make an aesthetic judgment, whether or not it concerns the perceived beauty or ugliness of an object. Regarding the visual aspect of art appreciation, the occipital areas including the bilateral occipital gyri (Vartanian & Goel, 2004), the middle occipital gyrus (Vartanian & Skov, 2014) and the lateral occipital gyrus (Di Dio et al., 2007) have all been observed to be involved in aesthetic appreciation of visual art, as well as the parahippocampal gyrus and fusiform gyrus (Vartanian & Skov, 2014), the parahippocampal place area (Yue et al., 2007) and the bilateral fusiform gyri (Vartanian & Goel, 2004). Furthermore, the amygdala and insula (e.g. Adolphs & Tranel, 1999; Changeux, 2012; Di Dio et al., 2007; Gosselin et al., 2007; Ishizu & Zeki, 2013; Vartanian & Skov, 2014) seem to be crucial components for the emotional aspect of feeling something when looking at art. Also, certain structures within the reward-system seem to be involved in the appreciation of visual art (e.g. Nadal & Pearce, 2011; Vartanian & Goel, 2004; Vartanian & Skov, 2014), suggesting that some artworks are more satisfying than others to look at, implying specific preferences that are highly individual and varying in relation to context (Vessel et al., 2009; Vessel & Rubin, 2010). Aesthetic appreciation then seems to be a highly complex feature of human cognition, consisting of neural networks interacting with each other, combining bottom-up sensory processing and top-down cortical processing, as well as visual processing of objects, places and faces, and the rewarding sensation of enjoyment upon looking at such visual content, possibly acting as a motivator toward survival or reproduction.

According to Pearce et al. (2016), there are three main reasons why neuroaesthetics have been met with much criticism from other scientific disciplines. First of all, there is a common belief that art and aesthetics are only valuable as sophisticated leisure activities. Secondly, there is the problem of subjectivity which is involved in all aesthetic experiences. Third, a biological theory of aesthetic experiences may not be needed in addition to a psychological one. Regarding the first reason, the majority of people today all engage in some activities where art is present, as aesthetic production and appreciation are natural features of human behavior. The modern use of art derives from the eighteenth century philosophy of fine art, which consisted of artworks mainly produced for the wealthy elite of the church and court, thereby laying elitist Eurocentric conceptions upon the practices of fine art (Brown & Dissanayake, 2009). This is somewhat reflected in today's modern society in the sense that some people tend to bypass this fundamental feature of human cognition and behavior, not considering art as something that may actually be meaningful to engage in outside its 'proper' environments, such as museums, art galleries, concert halls and similar activities (Pearce et al., 2016). In a sense, knowledge about the neural correlates and cognitive mechanisms of aesthetic appreciation is then of interest to cognitive neuroscience and psychology (Pearce et al., 2016). Regarding the second reason, empirical aesthetics seek out objective truths about aesthetic experiences, but the subjectivity that is inevitably inherent in an aesthetic experience cannot and should not be reduced to objective data in terms of neural activity. The barrier between objectivity and subjectivity has been noticed by some researchers and should be tried to overcome, as neuroaesthetics needs to examine whether or not these obstacles are “insurmountable in principle” (Nadal & Pearce, 2011, p. 181). According to some, science is unable to access aesthetic experiences in principle due to its experimental and pragmatic nature (e.g. Massey, 2009), since the very essence of the humanistic exploration of art is the subjectivity of individual experiences (Nadal & Pearce, 2011). However, from a methodological point of view, subjectivity is important to use alongside different approaches such as phenomenology and experimental psychology, ultimately with the aim to understand the mind. Therefore, subjectivity should not be discounted for in terms of understanding the neural underpinnings of aesthetic experience, as it is “simply one more tool” (Pearce et al., 2016, p. 269). Regarding the third reason, there have been debates about whether or not neuroaesthetics is a meaningful topic of interest, when there are already psychological models and frameworks that have contributed to our understanding of aesthetic appreciation and its relation to the human mind, such as the work of Fechner (1876), Berlyne (1974), Chatterjee and Vartanian (2014) and Leder et al. (2004). Some philosophers have dismissed and criticized neuroaesthetics for its methodological restrictions, accusing the reductionist and quantitative character of empirical aesthetics for not being able to meaningfully contribute to a significant understanding of art (Nadal et al., 2013). According to Pearce et al. (2016), neuroaesthetics is needed in addition to psychological research because of its complementary nature to psychological models, since empirical aesthetics and psychophysics are only explaining mental and psychological processes (Fechner, 1876; Berlyne, 1974); thus, they are incomplete and in need of biological foundations as well. Pearce et al. (2016) therefore means that the contribution of cognitive neuroscience to empirical aesthetics can be seen as, for example, the contribution of cognitive neuroscience of language to psycholinguists, or put in other words, as providing “a whole new suite of research tools and methods to the armory of the empirical aesthetician” (p. 273). The modern tools of cognitive neuroscience are then of great value to psychologists, who ultimately aim for the understanding of the cognitive and affective processes of the mind.

Unfortunately, there tend to be more problems for neuroaestheticians to solve, as well. Another recurrent problem is that empirical aesthetics, when practiced within neuroscience, often takes aesthetic objects out of their social, cultural and historical backgrounds, thereby ignoring important aspects that are individual to each observer (Nadal et al, 2013; Nadal & Pearce, 2011; Tallis, 2008; Zaidel et al., 2013). In neuroaesthetics, sets of stimuli or individual stimuli are being treated in isolation, cut apart from the observer's cultural context and individual history. This is problematic because it hinders the contribution to understanding why we think and feel the way we do when we experience art (Tallis, 2008). When conducting experiments in neuroaesthetics, all the lines, shapes, forms and colors that essentially make up the perceived wholeness of a painting are therefore not representing the beauty, sadness or tragedy that is such essential parts of human life. In other words, one might go as far as stating that neuroaesthetics is only a way of showing what lightens up in the brain when we see a colorful painting and nothing more, or as Tallis (2008) has eloquently put it:

> They [works of art; my note] invite us not only to have experiences but to reflect on our experiences; not merely to have visual tingles but to think about what is before us. In the case of representational works, we are invited to reflect on what is shown, to accept or refuse the symbolic significance, to rejoice in the beauty of the world or deplore its horror. The extraordinary sequence of Rembrandt self-portraits is not merely a succession of lines and coloured surfaces but a profound meditation on the course and tragic beauty of human life. An array of pixels or voxels, lit up or not, hardly captures that. (p. 19)

Advances in neuroaesthetics have often been backed by certain claims that most art can be accounted for in terms of neural mechanisms and networks (Hyman, 2010). However, reducing an aesthetic experience to neurobiological mechanisms will then fail in terms of explaining what distinguishes a genuinely aesthetic experience from perceptual experiences that are part of everyday life (Nadal & Pearce, 2011). If neuroaestheticians accept that they cannot reduce aesthetic experiences to decontextualized laboratory tasks, they must also accept that the results that are found and obtained in the lab are not sufficient to predict, or explain, what constitutes every other aesthetic experience that is happening outside of the experimentally controlled environment that these experiences are measured in (Nadal & Pearce, 2011).

There are also definitional problems of various natures. Brown and Dissanayake (2009) have recently stated the importance of the inherent ambiguity in the terms ‘art’ and ‘aesthetics’, as it might be that many scientists are currently employing these words in the wrong way, not taking into account their actual meanings from a historical and semantic viewpoint; essentially mixing up the meaning of the words. Brown and Dissanayake (2009) therefore state that a more broader and comprehensive understanding of art must include all kinds of artworks that are not exclusively bound to Western culture and art practices, spanning across all human cultures, forcing us to include all concepts within art that are not necessarily connected to beauty but to other concepts as well. Pearce et al. (2016) have recognized this problem too and very recently argued that neuroaesthetics should not limit itself to art but stretch its scope to a much wider range of sensory experiences and not just sensations of beauty, attempting to study a greater variety of aesthetic experiences. Furthermore, they argued that the cognitive neurosciences of aesthetics, beauty and art are all intersected with each other since they can relate to each other but not be limited to their respective fields. Aesthetic experiences can therefore be related to beauty but not limited to it alone, and cognitive neuroscience of art can be approached from several angles since it investigates the neuro-cognitive underpinnings of the creation and appreciation of art (Pearce et al., 2016). Thus, the field of aesthetic appreciation is multifaceted and should therefore be approached in different ways and techniques, allowing for the expansion of the field.

Future Challenges and Approaches within Neuroaesthetics

The goal for neuroaesthetics should not be to pinpoint the aesthetic value of objects but to gain a deeper understanding about the psychological and neural processes that underlie an individual's aesthetic sensory experience in different contexts, focusing on both the aesthetic object and the interaction between the context and individual (Pearce et al., 2016). Lab-based studies that use artificial stimuli allow for great experimental control but will lack in ecological validity. Thus, results should not be seen as complete but as complementary to studies of people in genuine aesthetic experiences and situations which have high ecological validity but may contain other confounding factors or additional noise, not allowing for great experimental validity (Pearce et al., 2016). This would be something to consider for future studies as the field continues to grow and mature.

Future endeavors should involve more attempts at bringing together research from different approaches, such as evolutionary psychology, cognitive neuroscience and behavioral psychology, in order to maintain a truly comparative and empirical understanding of aesthetic experiences. Researchers should try and move beyond voxels or slices of brain data, as the mere localization of brain areas can only provide *some* insights into what constitutes an aesthetic experience in terms of neural activity. Important directions that neuroaestheticians should explore involve investigating the time course of brain activation that is directly associated with an aesthetic experience, as well as the identification of "genuine modality-independent processes" which are "distinct from modality-specific ones" (Nadal & Pearce, 2011, p. 181). As known, there is no single brain region or area that can directly explain the relationship between aesthetic appreciation and brain activity (Zaidel, 2010). This contrast may serve to reflect the vast complexity of art and that all its parts and units are not so easily defined, suggesting the presence of a wide variety of brain areas and networks that underlie artistic talent, production and appreciation of art (Zaidel, 2010).

Although the typical driving force of all these types of studies is the goal of underpinning the neural correlates of aesthetic behavior, there are still different methodologies, theoretical backgrounds and stimuli used to investigate this particular issue (Nadal & Pearce, 2011). If researchers in neuroaesthetics investigate the neural foundations of aesthetic experience, they must be able to a) clarify and define what an aesthetic experience is, b) come up with a conceptual understanding of how such an experience relates to the workings of the brain, and c) make an identification of what the sources are that contribute to an aesthetic experience (Pearce et al., 2016). These are crucial aspects that need to be taken into account for the development of future studies, frameworks and models; all of which attempt to ultimately determine the cognitive and neural mechanisms that underlie aesthetic behavior.

Conclusions

In this thesis it has been shown that aesthetic appreciation of visual art seems to be involved with the activity of certain areas of the human brain. Some of these areas and structures are the prefrontal cortex, amygdala, insula, parahippocampal place area and the fusiform gyri. Also, reward-related structures and stimulus-specific triggered parts of the visual system have shown to be involved, as well. The neural foundations of aesthetic appreciation seem to be strongly involved with interactions between these aforementioned brain areas, as seen by the collected evidence. Furthermore, it has been shown that some brain deficits can change aesthetic taste across different sensory experiences such as visual art, music, and literature. The studies that have been reviewed in this thesis and their respective results continue to support the involvement of not one specific brain area in aesthetic appreciation, but rather several areas and structures that are related to the perception, evaluation and judgment of an aesthetic object. Moreover, problems that are of conceptual, methodological and definitional character have been brought up in order to shed light on the most important obstacles in neuroaesthetics, as well as possible solutions.

Future studies need to clearly address what aesthetic experiences are, what their conceptual relations to the brain might be, and in what way such experiences might best be pursued in terms of neural correlates and interactions. Even though aesthetic experiences differ greatly among people and are never the same twice, this does not mean that they are outside the scope of science. It only means that this research must seek out to determine and explain the individual differences in such experiences, and what those factors are at different moments and in different circumstances, in order to maintain the mature growing of a field that is new and exciting, working cross-culturally and interdisciplinary, with the goal to understand the psychological and neural processes that underlie having an aesthetic experience in a given context. It can be concluded, in the light of all the studies and their results that have been featured in this thesis, that neuroaesthetics is an important field to study in order to learn more about the neural underpinnings of art appreciation, as well as artistic production.

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