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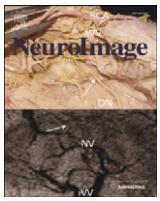

Naturalizing aesthetics: Brain areas for aesthetic appraisal across sensory modalities

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ABSTRACT

We present here the most comprehensive analysis to date of neuroaesthetic processing by reporting the results of voxel-based meta-analyses of 93 neuroimaging studies of positive-valence aesthetic appraisal across four sensory modalities. The results demonstrate that the most concordant area of activation across all four modalities is the right anterior insula, an area typically associated with visceral perception, especially of negative valence (disgust, pain, etc.). We argue that aesthetic processing is, at its core, the appraisal of the valence of perceived objects. This appraisal is in no way limited to artworks but is instead applicable to all types of perceived objects. Therefore, one way to naturalize aesthetics is to argue that such a system evolved first for the appraisal of objects of survival advantage, such as food sources, and was later co-opted in humans for the experience of artworks for the satisfaction of social needs.

Introduction

The notion of "the aesthetic" is a concept from the philosophy of art of the 18th century according to which the perception of beauty in sublime artworks occurs by means of a special process distinct from the appraisal of ordinary objects, for example food items (Goldman, 2001; Guyer, 2005). Hence, our appreciation of a painting is presumed to be cognitively distinct from our appreciation of an apple. This is due in part to our "disinterested" approach to the painting, in other words our emotional detachment from the painting due to its lack of practical use. The field of "neuroaesthetics" has adopted this distinction between art and non-art objects by seeking to identify brain areas that mediate the aesthetic appreciation of artworks, generally works from the domain of visual art (Zeki, 1999; Di Dio and Gallese, 2009; Skov, 2009; but see Brown and Dissanayake, 2009, and Vartanian, 2009).

However, studies from neuroscience and evolutionary biology challenge this separation of art from non-art, and instead call for a naturalization of aesthetics, in other words a revised conception of aesthetic processing that is more biological and adaptive in scope. Human neuroimaging studies have convincingly shown that the brain areas that mediate aesthetic responses to artworks overlap those that mediate the appraisal of objects of evolutionary importance, such as the desirability of food items or the attractiveness of potential mates. Hence, it is likely that artworks have co-opted the neural systems that subserve these kinds of adaptive assessments rather than having evolved a distinct type of neural processing. In addition, while "the aesthetic" of Enlightenment philosophy places

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an exclusive focus on positive-valence assessments – and thus beauty – aesthetic processing is best thought of as a binary phenomenon, with both positive and negative counterparts. Thus, negative-valenced emotions such as dislike and disgust are just as much aesthetic emotions as are awe and ecstasy. Aesthetic processing, at its core, can thus be equated with *object-appraisal* processes, resulting in emotions that sit along the spectrum from transcendence to repulsion. When seen in this way, aesthetic emotions become major factors in guiding motivation and decision making. We would thus expect neural pathways for object appraisal to involve areas not only for object perception but those for homeostatic processing, emotion, motivation, and motor control as well.

An important step towards naturalizing aesthetics is to ground aesthetic emotions in theories of emotion more generally. The standard model of emotion in psychology and biology – the basic emotion theory – offers little insight into aesthetics since it contains no primary emotion for positive-valenced appraisals such as pleasure, although it does include the negative-valenced counterpart of disgust (Ekman, 1992). The only positive-valenced emotion in the basic emotion theory is happiness, an emotion that is often conflated with pleasure. An influential alternative to the basic emotion theory, that put forward by Ortony et al. (1988), makes clear that aesthetic pleasure is an *object*-related emotion, whereas happiness is an *outcome*-related emotion. Hence, aesthetic emotions such as pleasure and repulsion are qualitatively distinct from outcome-related emotions such as happiness and disappointment.

This distinction between objects and outcomes figures prominently in neuroscience as well. Rushworth et al. (2008) presented a neural model of decision-making based on the notion that the appraisal of objects (what they refer to as "stimuli") is most strongly associated with the orbitofrontal cortex (OFC), whereas the appraisal of outcomes (what they refer to as "actions") is most strongly associated with the anterior cingulate cortex (ACC), and that these two appraisals can be doubly dissociated through lesions in animals. This is consistent with neuroanatomical studies showing that the OFC is a form of higher-level sensory cortex receiving input from "what" sensory pathways involved in object processing (Rolls, 2005), whereas the ACC is a premotor area involved in predicting and monitoring outcomes in relation to motivational intentions (Carter and van Veen, 2007). Hence, the object/outcome dichotomy makes important predictions about aesthetic processing, suggesting that aesthetic emotions should be primarily associated with object-appraisal mechanisms in the OFC.

There is, in fact, an abundant neuroimaging literature in humans (most of it distinct from the neuroaesthetic banner) showing that the OFC is reliably activated during tasks that require people to make appraisals of the quality of objects, both art and non-art objects (Kringelbach, 2005; Wallis, 2007). This would suggest that the OFC is a prime candidate for being the "aesthetic center" of the human brain. But the situation is more complicated than that. First, the OFC plays a prominent role in general sensory processing, being a secondary sensory cortex for both olfaction and gustation (Kringelbach, 2004; Rolls, 2004). Second, it serves a role in polysensory convergence, not least in the interaction between olfaction and gustation during "flavor" processing. Third, the OFC processes emotions of both valences, and there is no clear understanding of how positive- and negative-valenced appraisals are represented in the OFC.

Our goal in this study was to apply quantitative meta-analysis techniques to a comprehensive corpus of human neuroimaging studies of aesthetic processing across multiple sensory modalities and across both non-art and art objects. We were interested in seeing if there was indeed a supramodal brain area that is active during the process of object appraisal. The OFC was clearly our strongest candidate for such an area. Therefore, one of the major questions we wanted to address was whether regions of OFC activation across sensory modalities were overlapping or instead sensory-specific.

Methods

Inclusion criteria for papers

Meta-analysis of 93 published neuroimaging studies was performed using "activation likelihood estimation" (ALE) analysis. The studies are summarized in Supplementary Tables 1 and 2. They included papers that performed ROI-based and correlational analyses in addition to standard activation analyses. Database searches were carried out by the first three authors using search terms such as "aesthetics", "aesthetics + fMRI", "aesthetics + orbitofrontal" and "aesthetics + insula". In addition, extensive use was made of the Web of Knowledge database in order to find articles citing ones we already had. All three authors had to agree on the suitability of a paper for it to be included in a meta-analysis.

Our inclusion criteria for articles were: 1) that whole-brain analyses were performed, using either functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) (thereby excluding electrophysiology-based studies; ROI-based analyses were taken from whole-brain studies); 2) that the papers provided either Talairach or Montreal Neurological Institute (MNI) coordinates for their activation foci (thereby excluding papers that reported activations using neuroanatomical labels alone); 3) that the subjects were healthy individuals and not part of clinical populations (thereby excluding studies on, for example, depressed patients or individuals with feeding or body-perception disorders, such obese individuals or anorexics); 4) that the tasks involved some type of aesthetic evaluation of the presented stimuli, including ratings of pleasantness, attractiveness, and liking (thereby excluding studies of general sensory processing, decision making alone, or studies in which no explicit aesthetic appraisal was made by subjects); and 5) that task appraisals were of positive valence (thereby excluding studies of disgust, pain, noxious quality, unpleasantness, and the like). While the issue of negative valence is of central relevance to our approach to aesthetics, there were not enough papers across the five major sensory modalities to justify doing a parallel set of meta-analyses for negative-valence processing at the present time. Some of the studies that were included in the meta-analyses performed comparisons between positive- and negative-valence assessments, but we only selected the positive-valence tasks from those papers.

To elaborate further on our exclusion criteria, we excluded papers that did not place a central focus on aesthetic evaluation. This included studies that were primarily devoted to decision making, studies that were focused on learning and conditioning, studies that used rewarding stimuli as primes for other cognitive tasks, studies that used aesthetic-connoting words only, studies that had people state preferences among two choices, and studies that focused on reward processing in neuroeconomic experiments. In addition, we excluded studies of valence or arousal processing in which no ratings of pleasantness or attractiveness were made by subjects. This exclusion covered many studies of picture processing, including those of erotic stimuli.

While the distinction between "liking" and "wanting" is one that is frequently discussed in the neural literature on reward processing (Berridge and Kringelbach, 2009; Berridge et al., 2009), we do not consider this distinction here, as most of the studies looked at ratings of pleasantness or attractiveness. Hence, the focus was more on hedonic value (liking) than incentive value (wanting) or preference.

Activation likelihood estimation (ALE) analysis

Four parallel ALE meta-analyses were performed for four major sensory modalities, respectively: 1) vision (56 papers, 242 foci across the whole brain); 2) audition (8 papers, 95 foci); 3) gustation (16 papers, 136 activation foci); and 4) olfaction (13 papers, 109 foci). These are summarized in Supplementary Table 2. The vision category