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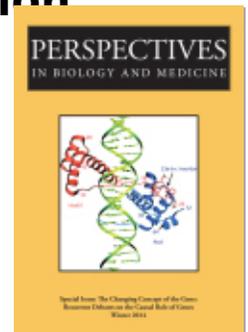
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## **The Artful Mind: Sexual Selection and an Evolutionary Neurobiological Approach to Aesthetic Appreciation**

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# THE ARTFUL MIND

## *sexual selection and an evolutionary neurobiological approach to aesthetic appreciation*

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DIRK DE RIDDER\* AND SVEN VANNESTE†

**ABSTRACT** Based on functional imaging of beauty appreciation in art and of beautiful faces, a heuristic model is presented that proposes that beauty appreciation in art is based on a sexual selection mechanism that led to the preference of beautiful faces. Beauty is linked to sexual selection as a sign of fitness. Beautiful traits, like the peacock's tail, are costly and thereby signal superior genetic quality. Mechanistically, beauty is a construct of the brain that links positive feedback of the reward system with hedonic experience, namely pleasure, which itself might be encoded in the orbito-frontal cortex. The context determines whether a stimulus should lead to further approach or withdrawal in order to maintain a hedonic homeostasis. The fact that aesthetic appreciation of art uses the same circuitry as the aesthetic appreciation of faces suggests that there is no special art circuitry in the brain, but that available networks are used for aesthetic appreciation of art.

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THE EARLIEST ANATOMICALLY modern humans in Europe are thought to have appeared around 43,000 to 42,000 years ago (Higham et al. 2011), and the oldest paintings in the Nerja caves in Spain date back to the same period, antedating the 33,000-year-old beautiful wall paintings in the Chauvet cave of the Ardeche region in France. This is in sharp contrast to the first written words, which date back to only to about 3200 BCE from Ancient Mesopotamia, Egypt, and China. Since pictorial representation predates written language, it has been suggested that these cave paintings are not “art” per se, but very early forms of information communication (Humphrey 1998; Mithen 1999). Interestingly, chimpanzees can create pictorial representations even though they cannot write, indirectly supporting this concept (Morris 1962). Analogous to evaluating pictorial art as a form of information communication, beauty can also be informative. A beautiful face, like the beautiful tail of a peacock, can serve a sign of fitness, indirectly demonstrating a genetic superiority related to parasite resistance and hence a form of sexual selection (Slavin 2011).

In this article, we review the neural correlates of the aesthetic appreciation of art and demonstrate that similar brain circuitry is used as for the aesthetic appreciation of faces. We suggest that art appreciation may therefore be an evolutionary by-product of this latter capacity, and thus related to sexual selection.

#### WHY STUDY BEAUTY AND NOT ART?

The concept of art appreciation is twofold. On the one hand, the aesthetic aspects of art are thought to please the senses, as Thomas Aquinas, in the *Summa Theologica*, stated in the Middle Ages. These aspects are usually investigated by psychologists and neuroscientists. On the other hand, art historians, starting with Pliny the Elder in the first century, analyze art in its historical context. With the creation of Andy Warhol’s famous *Brillo Boxes* in 1964, however, it has become impossible to define art. As Arthur Danto states, in an interview referring to his book *After the End of Art* (1997): “You can’t say something is art or not art anymore. That is all finished. Warhol made it no longer possible to distinguish something that is art from something that is not” (Menand 1998). This results in a problem for the science of art, as it is difficult to scientifically investigate something that cannot be defined.

Consequently, most neuroscientists have limited themselves to investigating beauty, which can at least be operationally defined. The Pythagorean definition sees beauty as a matter of mathematical symmetry and proportion, compressed into the  $\Phi$  ratio, also known as the golden ratio or golden mean. Beauty can also be defined in a Thomistic way as *id quod visum placet*, or that which pleases upon seeing it. Finally, beauty can be defined through a combination of both Pythagorean objective and Thomistic subjective measures, as proposed by Immanuel Kant.

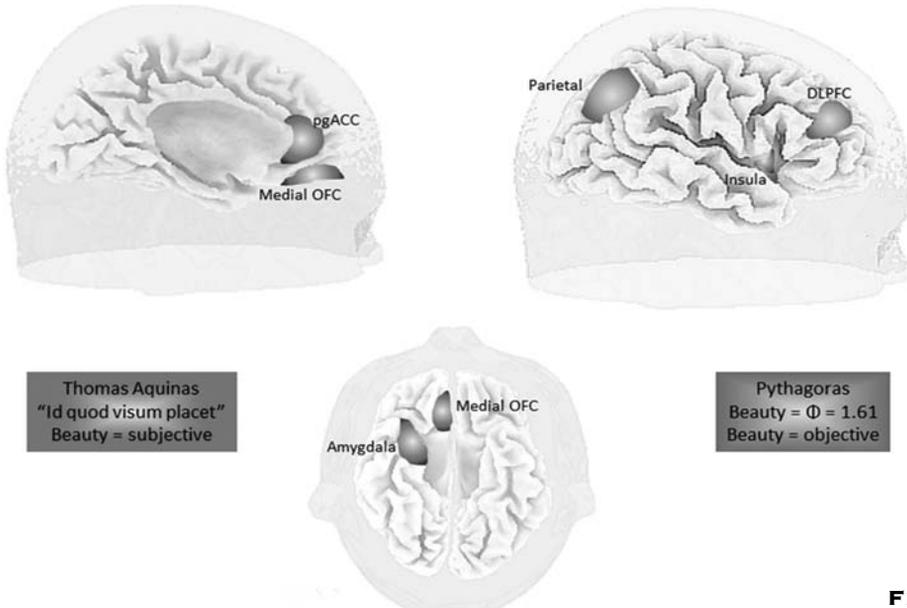


FIGURE 1

*Neural correlates of Thomistic (subjective) and Pythagorean (objective) beauty. Combining the subjective and objective correlates of beauty would create the neural correlates of Kantian beauty.*

### PYTHAGOREAN, THOMISTIC, AND KANTIAN APPROACHES TO BEAUTY

Pythagorean or objective beauty has been studied by looking at the *Doryphoros*, a statue of a male athlete that was sculpted by Polycleitus in about 400–450 BCE (Di Dio, Macaluso, and Rizzolatti 2007). Its form contains  $\Phi$  ratios between the head and umbilicus and the umbilicus and the feet, and between the feet and knee and the knee and umbilicus. If these  $\Phi$  ratios are altered to generate a dysmorphic statue, one that has short legs and long trunk, it will no longer be perceived by most viewers as beautiful: while the canonical statue is judged as beautiful 76% of the time, the dysmorphic statue is scored as ugly 63% of the time. The neural correlates of the objective canonical beauty are represented by activation in the right dorsolateral prefrontal cortex, right parietal cortex, left anterior cingulate cortex, and right insula. The right dorsolateral prefrontal cortex-parietal activation likely represents cognitive appraisals or attention, while the anterior cingulate cortex and insula likely represent the salience of the artwork (Corbetta and Shulman 2002; Seeley et al. 2007; Vincent et al. 2008). Cognitive aspects of art appreciation are represented by frontoparietal activity (Cupchik et al. 2009). (See Figure 1, left panel.)

The subjective Thomistic appraisal of the statue correlates with right amygdala activation, but also with orbitofrontal activation (Di Dio, Macaluso, and Rizzolatti 2007; Kawabata and Zeki 2004). The beauty of a painting, irrespec-

tive of the type, correlates with orbitofrontal activity, and the more beautiful it is perceived to be, the higher the activity (Brown et al. 2011; Ishizu and Zeki 2011). This is analogous to what has been found for music. Indeed, the emotional appraisal of beauty is related to activity of an overlapping network, irrespective of the sensory modality by which it is perceived. The network consists of the orbitofrontal cortex, insula, and pregenual anterior cingulate cortex. The medial orbitofrontal cortex activation might be related to an approach behavior to the beauty of the stimulus, the insula to its salience, conscious perception, or autonomic response, and the pregenual anterior cingulate cortex activity to the hedonic aspect (Craig 2002; Elliott, Dolan, and Frith 2000; Hasler et al. 2008; Oppenheimer et al. 1992; Seeley et al. 2007; Walter et al. 2009). (See Figure 1, right panel.)

The Kantian definition of beauty, expressed in his *Critique of Judgment* (1790), reflects a combination of cognitive (beautiful) and emotional (sublime) appraisals of art, which might be evaluated by the neural correlates of abstract beauty. It has been shown that for art experts, in contrast to non-experts, abstract art has equal emotional valence and aesthetic value as figurative art (Pihko et al. 2011). The differences in brain activity when judging abstract beauty versus symmetry in art are represented by activity in the right anterior cingulate cortex and bilateral insula, which are involved in salience; the right dorsal medial prefrontal cortex, which is involved in judgment (Moll, Eslinger, and Oliveira-Souza 2001); the bilateral ventrolateral prefrontal cortex and left temporal pole, which are involved in context (Kirk et al. 2009); and the bilateral temporoparietal junction, right posterior cingulate, and left precuneus, which together with the dorsal medial prefrontal cortex have been implicated in self-perception and possibly self-related evaluation of the presented art (do I find this picture beautiful? Jacobsen et al. 2006).

The question arises whether these beauty-related networks are specific for art, or whether they are more generic. If so, this could cast doubt on the concept that beauty appreciation in art epitomizes a culmination of human evolution and may suggest that beauty appreciation should be explained rather as a potential side-product of something else, related to natural or sexual selection. We hereby propose that aesthetic appreciation of art uses the same circuitry as the aesthetic appreciation of beautiful faces, which have been considered evolutionary reflections of good health, important in sexual selection. The components of the “beauty appreciation” networks should therefore be explainable in generic sub-networks important for survival and procreation.

#### **EPICURISM AS A NEUROBIOLOGICAL MECHANISM OF LIFE**

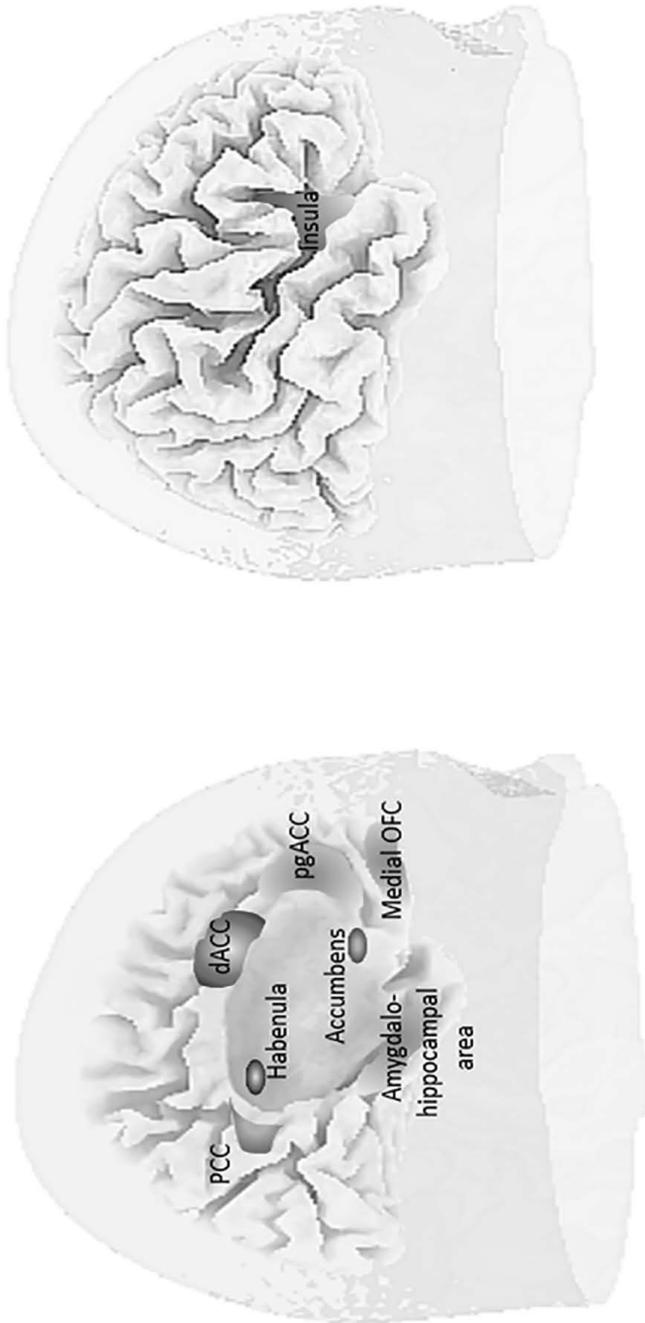
Epicurism (based on Plato, Aristotle, and Democritus) proposes that the pursuit of pleasure and absence of pain, but without excesses, is the purpose of life. It

contains the elements of *ataraxia*, which is the peace and freedom from fear, and *aponia*, which is the absence of pain. Bentham and John Stuart Mill's utilitarianism extends this principle to the idea that one has to maximize pleasure and minimize pain. The neurobiological approach suggests that the pain/pleasure contrast is not only the purpose of life but might actually be a mechanism of life.

The brain can be considered as a prediction machine that uses information from previous experiences to predict future events in order to reduce uncertainty (De Ridder, Vanneste, and Freeman 2012). It has been suggested that our brain works in a Bayesian way and tries to reduce environmental uncertainty, based on the free-energy principle, which has been proposed as a universal principle governing adaptive brain function and structure (Friston 2010). The free-energy principle states that the brain must minimize its Shannonian free-energy—in other words, it must reduce by the process of perception its uncertainty (its prediction errors) about its environment. This optimization is important for survival. As such the “Bayesian brain” can be conceptualized as a probability machine that constantly makes predictions about the world and then updates them, based on what it actively explores in the environment by means of the senses (Knill and Pouget 2004).

There is an inbuilt feedback mechanism, partially mediated by the reward system, that compares the prediction to what is actively sensed in the environment and gives either a positive or a negative feedback. This feedback mechanism comprises subcortical structures, such as the nucleus accumbens and the posterior cingulate cortex for positive feedback, and the habenula, dorsal anterior cingulate cortex, and anterior insula for negative feedback (Ullsperger and von Cramon 2003). (See Figure 2.) When these structures are connected or co-activated with the orbitofrontal cortex, they are expected to give rise to feelings such as pleasure or pain. The larger networks encoding pain and pleasure largely overlap, and thus from an evolutionary point of view, negative feedback equals pain, while positive feedback equals pleasure (Leknes and Tracey 2008). This suggests that pleasure and displeasure are signs of the physiological usefulness of a stimulus, or in the words of Democritus, “Joy and sorrow are the distinguishing mark of things beneficial and harmful” (Taylor 2005). Pleasure is a force that orients behavior to approach and consume the stimulus, so that, in the words of Aristotle in the *Nicomachean Ethics*: “One may also think that, if all humans seek pleasure, that is because they desire to live” (Cabanac 2010, p. 115). It has been suggested that the drive, desire, or motivation is encoded by dopamine, whereas the pleasure is encoded by the opioid system (Berridge 2007; Berridge and Kringelbach 2008; Smith and Berridge 2007). The orbitofrontal cortex is ideally suited for integrating desire and pleasure, as it has connections to both dopamine and the opioid system.

As the brain has to calculate priority between multiple simultaneous needs and stimuli, it requires a common currency to compare these needs and stimuli, and it has been suggested that pleasure is the common currency (Cabanac 1992;



**FIGURE 2**

*Pain and pleasure encoding areas overlap. They encompass areas involved in negative and positive feedback, as well as other areas related to pain or pleasure. The pregenual ACC and orbitofrontal cortex are related to hedonic feelings; the amygdalohippocampal area to emotional and pain memory.*

McFarland and Sibly 1975). In other words, opioid-mediated pleasure is intrinsically linked to a dopaminergic-related motivational capacity of consciousness. A positive feedback thus leads to rewarding a stimulus, motivating the individual to obtain more of the same stimulus. In this sense, pleasure can be analogous to beauty, appetite, and other drives that lead to approaching behavior, while pain is analogous to repulsion, disgust, and other drives leading to withdrawal. Neurobiologically, approach behavior is linked to medial orbitofrontal activity, and withdrawal is linked to lateral orbitofrontal activity (Elliott, Friston, and Dolan 2000). The appeal of visual art involves activation of reward circuitry, and the reward activation is based on artistic status alone (in other words, it is specific for art), independently of its hedonic value (Lacey et al. 2011). This is analogous to Kant's statement in the *Critique of Judgment* that "beauty pleases immediately . . . apart from all interest," and it might also explain the "art infusion" effect, namely that products sell better when advertised with art (Hagtvedt 2008).

But as mentioned, pleasure and pain depend on the context: a heat stimulus is pleasant when it is cold, but unpleasant when it is hot (Mower 1976). This contextual influence is essential for system stability and can be considered a mechanism of physiological homeostasis, also hedonic homeostasis. When hungry, appetite/pleasure tells you to continue eating, but when homeostatic balance is reached, satiety tells you that you have had enough food; when you overeat, repulsion and stomach pain arises from the same food stimulus that initially was pleasurable. In certain contextual situations, the seemingly antagonistic significance of pain and pleasure can cease, as in sadomasochism: masochists derive pleasure from receiving pain, but only certain kinds of pain in very specific contextual situations.

### A DARWINIAN APPROACH TO BEAUTY

One question that arises, however, is why beauty is linked to pleasure, as a mechanism of positive feedback? Darwin wrote to Asa Gray in 1860 that "The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" (Letter 2743, Darwin 1911). These words dramatically explain Darwin's frustration that beauty could not be explained by natural selection—on the contrary, it goes against natural selection. But he came up with a solution: beauty is linked to sexual selection, as a sign of fitness. Since certain traits are costly, they thereby signal superior genetic quality. In other words, sexual selection depends on the handicap principle (Smith 1976; Zahavi 1975). Reliable signals must be costly (wasteful, useless) to the signaler, costing the signaler something that could not be afforded by an individual with less of this specific trait. In the case of the peacock's tail, the tail signals to peahens that "I have survived in spite of this huge tail, hence I am fitter and more attractive than others." But the peacock is not the only creature for whom extravagant display pays off in mate

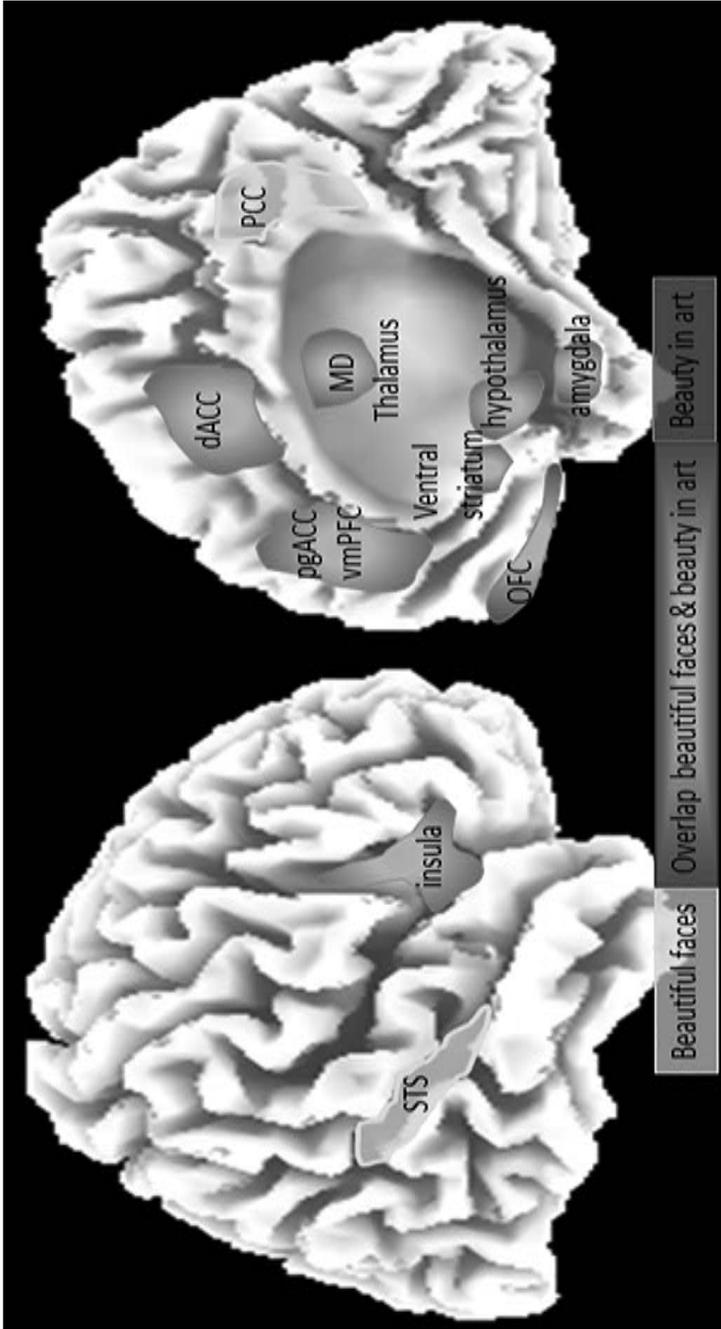
attraction. For barn swallows, the delay between arriving in a breeding area and attracting a mate is normally eight days. However, when tails are shortened, it takes 12 days, and when tails are lengthened it takes three days (Moller 1988). Similar signs of beauty and sexual selection have been demonstrated for African widowbirds, guppies, and platys (Andersson 1982; Basolo 1990; Bisschoff, Gould, and Rubenstein 1985).

When evaluating the aesthetics of art, the same networks are activated as for attractive faces, including the nucleus accumbens involved in the reward system; the amygdala, insula, and anterior cingulate cortex involved in emotion, salience, and autonomic nervous system control; the medial orbitofrontal involved in hedonic/beauty; the ventromedial prefrontal cortex, posterior cingulate cortex, and superior temporal sulcus involved in self-perception; and the dorsolateral prefrontal cortex-parietal cognitive control network art (Aharon et al. 2001; Brown et al. 2011; Chatterjee et al. 2009; Cupchik et al. 2009; Ishizu and Zeki 2011; Jacobsen et al. 2006; Kranz and Ishai 2006; Lacey et al. 2011). (See Figure 3.) Thus “art imitates nature,” as Aristotle wrote in his *Poetics*. The fact that aesthetic appreciation of art uses the same circuitry as the aesthetic appreciation of beautiful faces suggests that there is no special art circuitry in the brain, but that aesthetic appreciation of art uses networks that developed via sexual selection. The recognition of abstract paintings also uses structures that are nonspecific for art: trained people recognize more paintings correctly using networks associated with higher parahippocampal activity, analogous to other studies on recognition (Cabeza et al. 2001; Wiesmann and Ishai 2010).

The context determines how beautiful, or how positively rewarding, a certain piece of art is considered to be, and context in art, independent of its aesthetic value, correlates with bilateral activations of temporal pole and bilateral amygdalohippocampal area, analogous to semantic context processing in non-art tasks (Hoenig and Scheef 2005; Kirk et al. 2009). This context dependence is reminiscent of Merleau-Ponty’s (1945) concept of perception in general. He proposes that an object of perception cannot be seen in isolation because it is always embedded in a context: “If we turn back to the phenomena, they show us that the apprehension of a quality, just as that of size, is bound up with a whole perceptual context” (p. 9). It exists in relationship to other things, which is what gives it its meaning in the world. Thus, perception is the intentional sensing of information (looking for) within a context, and this also holds for art.

### PLATO’S TRINITY

A neurobiological evolutionary framework for the science of aesthetic appreciation should be scientifically testable and integrate aesthetic appreciation and ethics in one model. If beauty is a way of perceiving positive feedback about a stimulus, conceptually the same can be said of truth and goodness. Nietzsche was strongly influenced by Darwinism in his philosophical ideas and writings



**FIGURE 3**

*Overlapping areas between appreciation of beautiful faces and beauty in art. In appreciation of beautiful faces, the same areas are involved as in the appreciation of beauty in art, with the addition of the PCC and STS, possibly reflecting self/other perception.*

(Pence 2012). In *On Truth and Lies in a Nonmoral Sense* (1873), Nietzsche said that “Truth is nothing more than the invention of fixed conventions for merely practical purposes, especially those of repose, security and consistence” (cited in Wicks 1996). This suggests that truth might indeed be a positive feedback mechanism, in that the obtained information from the environment is “workable” in John Dewey’s (1916) sense of the word: it reduces the inherent uncertainty of the environment (De Ridder, Vanneste, and Freeman 2012). Thus, Keats’s epigram “beauty is truth and truth beauty” might indeed have neurobiological underpinnings (Harris, Sheth, and Cohen 2008). It is possible that beauty and truth reflect correctness of internal consistency, semantically for truth or image-like for beauty.

Nietzsche also stated in *Beyond Good and Evil* (1886) that “The falseness of a judgment is to us not necessarily an objection to a judgment. . . . The question is to what extent it is life-advancing, life-preserving, species-preserving, perhaps even species-breeding” (p. 3). It has been shown that beautiful people are considered good and accurate because beauty is desired (a sign of good health; Lemay, Clark, and Greenberg 2010; Lorenzo, Beisanz, and Human 2010). This predicts that the brain correlates of beauty and goodness overlap, as has been shown before (Zaidel and Nadal 2011).

Since the neural networks that involve appreciation of beauty, truth, and morality appear to be partially overlapping, Plato’s trinity of truth, goodness, and beauty appears to have a neurobiological underpinning grounded in evolutionary theory. More functional imaging-based research should explore this concept further. The neural correlates of truth, beauty, and goodness could be disentangled by evaluating each characteristic in artwork that contains both moral contents and beauty, both goodness and beauty, and so on. A conjunction analysis may demonstrate the overlapping networks and specificity of each aspect of Plato’s trinity.

### **CONCLUSION**

In summary, beauty is a construct of the brain, related to sexual selection linking positive feedback of the reward system with hedonic experience, namely pleasure, which itself might be encoded in the orbitofrontal cortex. The context determines whether a stimulus should lead to further approach or withdrawal in order to maintain a hedonic homeostasis, and the aesthetic appreciation of art uses the same circuits as the aesthetic appreciation of faces. As long as no operational definition of art exists, it might be scientifically easier to develop a neurobiological evolutionary framework for the science of aesthetic appreciation as performed in this review, instead of a framework for the science of art.

## REFERENCES

- Aharon, I., et al. 2001. Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* 32(3):537–51. doi: S0896-6273(01)00491-3 PII.
- Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature* 299:818–20.
- Basolo, A. L. 1990. Female preference predates the evolution of the sword in swordtail fish. *Science* 250(4982):808–10. doi: 250/4982/808 PII 10.1126/science.250.4982.808.
- Berridge, K. C. 2007. The debate over dopamine's role in reward: The case for incentive salience. *Psychopharmacol (Berl)* 191(3):391–431. doi: 10.1007/s00213-006-0578-x.
- Berridge, K. C., and M. L. Kringelbach. 2008. Affective neuroscience of pleasure: Reward in humans and animals. *Psychopharmacol (Berl)* 199(3):457–80. doi: 10.1007/s00213-008-1099-6.
- Bischoff, R., J. Gould, and D. Rubenstein. 1985. Tail size and female choice in the guppy. *Behav Ecol Sociobiol* 17:253–55.
- Brown, S., et al. 2011. Naturalizing aesthetics: Brain areas for aesthetic appraisal across sensory modalities. *Neuroimage* 58(1):250–58. doi: S1053-8119(11)00620-3 PII 10.1016/j.neuroimage.2011.06.012.
- Cabanac, M. 1992. Pleasure: The common currency. *J Theor Biol* 155(2):173–200.
- Cabanac, M. 2010. The dialectics of pleasure. In *Pleasures of the brain*, ed. M. Kringelbach and K. Berridge, 113–24. Oxford: Oxford Univ. Press.
- Cabeza, R., et al. 2001. Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. *Proc Natl Acad Sci USA* 98(8):4805–10.
- Chatterjee, A., et al. 2009. The neural response to facial attractiveness. *Neuropsychology* 23(2):135–43. doi: 2009-02621-001 PII 10.1037/a0014430.
- Corbetta, M., and G. L. Shulman. 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3(3):201–15. doi: 10.1038/nrn755 nrn755 PII.
- Craig, A. D. 2002. “How do you feel?” Interoception: The sense of the physiological condition of the body. *Nat Rev Neurosci* 3(8):655–66. doi: 10.1038/nrn894 nrn894 PII.
- Cupchik, G. C., et al. 2009. Viewing artworks: Contributions of cognitive control and perceptual facilitation to aesthetic experience. *Brain Cogn* 70(1):84–91. doi: S0278-2626(09)00009-8 PII 10.1016/j.bandc.2009.01.003.
- Danto, A. 1997. *After the end of art: Contemporary art and the pale of history*. Princeton: Princeton Univ. Press.
- Darwin, C. 1911. *The life and letters*, ed. F. Darwin. New York: Appleton.
- De Ridder, D., S. Vanneste, and W. Freeman. 2012. The Bayesian brain: Phantom percepts resolve sensory uncertainty. *Neurosci Biobehav Rev*. doi: S0149-7634(12)00060-7 PII 10.1016/j.neubiorev.2012.04.001.
- Dewey, J. 1916. What pragmatism means by practical. In *Essays in experimental logic*, ed. M. Hester and R. Talisse, 309–29. Carbondale: Southern Illinois Univ. Press, 2007.
- Di Dio, C., E. Macaluso, and G. Rizzolatti. 2007. The golden beauty: Brain response

- to classical and renaissance sculptures. *PLoS One* 2 (11):e1201. doi: 10.1371/journal.pone.0001201.
- Elliott, R., R. J. Dolan, and C. D. Frith. 2000. Dissociable functions in the medial and lateral orbitofrontal cortex: Evidence from human neuroimaging studies. *Cereb Cortex* 10(3):308–17.
- Elliott, R., K. J. Friston, and R. J. Dolan. 2000. Dissociable neural responses in human reward systems. *J Neurosci* 20(16):6159–65. doi: 20/16/6159 PII.
- Friston, K. 2010. The free-energy principle: a unified brain theory? *Nat Rev Neurosci* 11(2):127–38. doi: nrm2787 PII 10.1038/nrn2787.
- Hagtvedt, H. 2008. Art infusion: The influence of visual art on the perception and evaluation of consumer products. *J Marketing Res* 45:379–89.
- Harris, S., S. A. Sheth, and M. S. Cohen. 2008. Functional neuroimaging of belief, disbelief, and uncertainty. *Ann Neurol* 63(2):141–17. doi: 10.1002/ana.21301.
- Hasler, G., et al. 2008. Neural response to catecholamine depletion in unmedicated subjects with major depressive disorder in remission and healthy subjects. *Arch Gen Psychiatry* 65(5):521–31. doi: 65/5/521 PII 10.1001/archpsyc.65.5.521.
- Higham, T., et al. 2011. The earliest evidence for anatomically modern humans in northwestern Europe. *Nature* 479(7374):521–24. doi: nature10484 PII 10.1038/nature10484.
- Hoening, K., and L. Scheef. 2005. Mediotemporal contributions to semantic processing: fMRI evidence from ambiguity processing during semantic context verification. *Hippocampus* 15(5):597–609. doi: 10.1002/hipo.20080.
- Humphrey, N. 1998. Cave art, autism, and the evolution of the human mind. *Cambridge Archeol J* 8(2):165–91.
- Ishizu, T., and S. Zeki. 2011. Toward a brain-based theory of beauty. *PLoS One* 6 (7):e21852. doi: 10.1371/journal.pone.0021852 PONE-D-11-05060 PII.
- Jacobsen, T., et al. 2006. Brain correlates of aesthetic judgment of beauty. *Neuroimage* 29(1):276–85. doi: S1053-8119(05)00499-4 PII 10.1016/j.neuroimage.2005.07.010.
- Kant, I. 1790. *Critique of judgement*. New York: Oxford Univ. Press, 2007.
- Kawabata, H., and S. Zeki. 2004. Neural correlates of beauty. *J Neurophysiol* 91(4): 1699–705. doi: 10.1152/jn.00696.2003 91/4/1699 PII.
- Kirk, U., et al. 2009. Modulation of aesthetic value by semantic context: An fMRI study. *Neuroimage* 44(3):1125–32. doi: S1053-8119(08)01109-9 PII 10.1016/j.neuroimage.2008.10.009.
- Knill, D. C., and A. Pouget. 2004. The Bayesian brain: The role of uncertainty in neural coding and computation. *Trends Neurosci* 27(12):712–19. doi: S0166-2236(04) 00335-2 PII 10.1016/j.tins.2004.10.007.
- Kranz, F., and A. Ishai. 2006. Face perception is modulated by sexual preference. *Curr Biol* 16(1):63–68. doi: S0960-9822(05)01371-0 PII 10.1016/j.cub.2005.10.070.
- Lacey, S., et al. 2011. Art for reward's sake: Visual art recruits the ventral striatum. *Neuroimage* 55(1):420–33. doi: S1053-8119(10)01457-6 PII 10.1016/j.neuroimage.2010.11.027.
- Leknes, S., and I. Tracey. 2008. A common neurobiology for pain and pleasure. *Nat Rev Neurosci* 9(4):314–20. doi: nrm2333 PII 10.1038/nrn2333.
- Lemay, E. P., Jr., M. S. Clark, and A. Greenberg. 2010. What is beautiful is good because what is beautiful is desired: Physical attractiveness stereotyping as projection of

- interpersonal goals. *Perspect Soc Psychol Bull* 36(3):339–53. doi: 36/3/339 PII 10.1177/0146167209359700.
- Lorenzo, G. L., J. C. Biesanz, and L. J. Human. 2010. What is beautiful is good and more accurately understood: Physical attractiveness and accuracy in first impressions of personality. *Psychol Sci* 21(12):1777–82. doi: 0956797610388048 PII 10.1177/0956797610388048.
- McFarland, D. J., and R. M. Sibly. 1975. The behavioural final common path. *Philos Trans R Soc Lond B Biol Sci* 270(907):265–93.
- Menand, L. 1998. A critic at large. What is “art”? *New Yorker*, Feb. 9.
- Merleau-Ponty, M. 1945. *Phénoménologie de la perception*. Trans. P. Kegan. Paris: Gallimard.
- Mithen, S. 1999. *The prehistory of the mind: The cognitive origins of art, religion and science*. New York: Thames & Hudson.
- Moll, J., P. J. Eslinger, and R. Oliveira-Souza. 2001. Frontopolar and anterior temporal cortex activation in a moral judgment task: Preliminary functional MRI results in normal subjects. *Arq Neuropsiquiatr* 59(3-B):657–64.
- Moller, A. P. 1988. Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* 332:640–42.
- Morris, D. 1962. *The biology of art: A study of the picture-making behaviour of the great apes and its relationship to human art*. London: Methuen.
- Mower, G. D. 1976. Perceived intensity of peripheral thermal stimuli is independent of internal body temperature. *J Comp Physiol Psychol* 90(12):1152–55.
- Nietzsche, F. 1886. *Beyond good and evil*. New York: Dover, 1997.
- Oppenheimer, S. M., et al. 1992. Cardiovascular effects of human insular cortex stimulation. *Neurology* 42(9):1727–32.
- Pence, C. H. 2012. Nietzsche’s aesthetic critique of Darwin. *Hist Philos Life Sci* 33(2):165–90.
- Pihko, E., et al. 2011. Experiencing art: The influence of expertise and painting abstraction level. *Front Hum Neurosci* 5:94. doi: 10.3389/fnhum.2011.00094.
- Seeley, W. W., et al. 2007. Dissociable intrinsic connectivity networks for salience processing and executive control. *J Neurosci* 27 (9):2349–56. doi: 27/9/2349 PII 10.1523/JNEUROSCI.5587-06.2007.
- Slavin, K. V. 2011. Technical aspects of peripheral nerve stimulation: Hardware and complications. *Prog Neurol Surg* 24:189–202. doi: 000323275 PII 10.1159/000323275.
- Smith, J. M. 1976. Sexual selection and the handicap principle. *J Theor Biol* 57(1):239–42.
- Smith, K. S., and K. C. Berridge. 2007. Opioid limbic circuit for reward: Interaction between hedonic hotspots of nucleus accumbens and ventral pallidum. *J Neurosci* 27 (7):1594–605.
- Taylor, C. C. W. 2005. Democritus. In *The Cambridge history of Greek and Roman political thought*, ed. C. Rowe and M. Schofield, 125. Cambridge: Cambridge Univ. Press.
- Ullsperger, M., and D. Y. von Cramon. 2003. Error monitoring using external feedback: Specific roles of the habenular complex, the reward system, and the cingulate motor area revealed by functional magnetic resonance imaging. *J Neurosci* 23(10):4308–14. doi: 23/10/4308 PII.

- Vincent, J. L., et al. 2008. Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *J Neurophysiol* 100(6):3328–42. doi: 90355.2008 PII 10.1152/jn.90355.2008.
- Walter, M., et al. 2009. The relationship between aberrant neuronal activation in the pregenual anterior cingulate, altered glutamatergic metabolism, and anhedonia in major depression. *Arch Gen Psychiatry* 66(5):478–86. doi: 66/5/478 PII 10.1001/archgenpsychiatry.2009.39.
- Wicks, R. 1996. Frederick Nietzsche. In *The Stanford encyclopedia of philosophy*, ed. E. Zalta. <http://plato.stanford.edu/entries/nietzsche/>.
- Wiesmann, M., and A. Ishai. 2010. Training facilitates object recognition in cubist paintings. *Front Hum Neurosci* 4:11. doi: 10.3389/neuro.09.011.2010.
- Zahavi, A. 1975. Mate selection: A selection for a handicap. *J Theor Biol* 53(1):205–14. doi: 0022-5193(75)90111-3 PII.
- Zaidel, D. W., and M. Nadal. 2011. Brain intersections of aesthetics and morals: Perspectives from biology, neuroscience, and evolution. *Perspect Biol Med* 54(3):367–80. doi: S1529879511300038 PII 10.1353/pbm.2011.0032.