Evolutionary Psychology

www.epjournal.net – 2010. 8(4): 695-719

Original Article

Toward an Integrative Approach of Cognitive Neuroscientific and Evolutionary Psychological Studies of Art

Johan De Smedt, Department of Philosophy and Ethics, Ghent University, Ghent, Belgium. Email: johan.desmedt@ugent.be (Corresponding author).

Helen De Cruz, Centre for Logic and Analytic Philosophy, Katholieke Universiteit Leuven, Leuven, Belgium.

Abstract: This paper examines explanations for human artistic behavior in two reductionist research programs, cognitive neuroscience and evolutionary psychology. Despite their different methodological outlooks, both approaches converge on an explanation of art production and appreciation as byproducts of normal perceptual and motivational cognitive skills that evolved in response to problems originally not related to art, such as the discrimination of salient visual stimuli and speech sounds. The explanatory power of this reductionist framework does not obviate the need for higher-level accounts of art from the humanities, such as aesthetics, art history or anthropology of art.

Keywords: cognitive neuroscience, evolutionary psychology, art

Introduction

In recent years, cognitive neuroscientists and evolutionary psychologists have provided reductionist accounts of human behavior in terms of the lower-level theories and concepts of biology. Reductionism in scientific practice is primarily an *explanatory* strategy: Reductionist scientific explanations are not necessarily committed to the view that higher levels of explanation can always be reduced to more fundamental ones; rather, they attempt to gain a better understanding of a given phenomenon by focusing on a basic level of explanation. Unification, the ability to explain a wide range of phenomena using a relatively restricted set of premises, is arguably the most important of the explanatory goals of reductionist research programs (Steel, 2004). Evaluations of these programs should therefore assess to what extent they are successful in unifying a diversity of observations through a restricted set of principles. This paper examines to what extent two flourishing reductionist approaches to human behavior – cognitive neuroscience and evolutionary psychology – provide unifying explanatory frameworks to understand art and its aesthetic appreciation, and whether they obviate the need for higher-level accounts. Additionally, it explores to what extent theoretical evolutionary considerations can outline new directions for empirical research on art production and appreciation.

Art presents an ideal case study to evaluate reductionist programs, because it is a paradigmatic domain of investigation of the humanities, such as aesthetics, art history and art sociology which typically take a more holistic approach to the phenomena under investigation. Within and across these disciplines, there is little agreement on how art should be studied or defined. Although visual art (in the form of body decoration, artifact decoration, and often sculpture and painting), dance and music appear in all known human cultures past and present (Brown, 1991, p. 140), most indigenous languages lack a term equivalent to the western notion of art for art's sake, which only emerged in the late 18th century (Dutton, 2009). A radical solution to this definitional problem is to qualify only fine art, as it developed in post-Enlightenment Europe. But this merely shifts the problem of continuity: The functions, styles and social contexts of 19th-century art clearly differ from that of, say, the 1950s, which again radically differs from that of art today. On the other hand, Hellenistic sculptors, Gothic architects, and Melanesian wood carvers did not possess the modern western concept of art, yet we readily appreciate and appropriate their work. And just as sculptures from sub-Saharan Africa and Oceania adorn western homes, artists from these cultures have eagerly adopted western styles and media, as for example in historical ledger art (narrative drawings in pencil in ledger books by Native Americans of the Great Plains) or contemporary Australian aboriginal painting, which mixes indigenous themes with western media such as oil or acryl painting. Thus, even though people from those cultures do not have terms that are equivalent to our notion of art, they seem to recognize similarities between their and our artistic expressions. Moreover, many cultures have indigenous terms that capture aspects of the western concept of art, such as skill or beauty (Van Damme, 1997). Experimental studies (e.g., Seifert, 1992) show that western subjects without any formal training in art or aesthetics display and freely express aesthetic judgments on works of visual art, even if they are unfamiliar with them, like African sculpture. What is it that we intuit when we judge something to be a work of art?

Providing a concept of art that would allow us to discriminate art from non-art is an outstanding problem in contemporary philosophy of art – attempting a solution to this problem falls outside the scope of this paper. Also, this paper will not try to establish what factors contribute to artistic quality (i.e., what distinguishes "good art" from "bad art"). We do seem to have an intuitive, pretheoretical notion of what art may be (Osborne, 1981). Humans may possess a *folk concept of art* akin to folk biology and folk psychology: a tacit, inarticulate concept of what a work of art is like, which guides their identification of some objects and performances across cultures as art. This folk concept includes objects and performances that are typically manmade, that elicit aesthetic experiences[1], and that are embedded in social contexts. It is this broad folk concept of art that scholars across disciplines attempt to capture. Some (e.g., Davies, 2006) emphasize the aesthetic properties

[1] The term "aesthetic experience" refers to sensory and qualitative appreciation that involves a subjective sense of pleasure—it is not restricted to art, but can be elicited by other stimuli, like a well-made piece of furniture or a beautiful landscape.

of artworks, attempting to discriminate from other phenomenological experiences an aesthetic sensation, i.e., a subjective sensation of pleasure derived from sensory (usually visual or auditory) perception. Others, following Gell (1998), deliberately exclude aesthetics from their analysis and focus on the social role of art. Next to these, some philosophers of art (e.g., Levinson, 1993) prefer to examine artworks in terms of the intentions of their makers. None of these attempts have provided an adequate concept of art that captures all forms of human production that we intuit as art. For this reason, some philosophers of art (e.g., Mag Uidhir and Magnus, in press) propose to abandon the search for a unifying concept of art. In the light of this methodological and conceptual fragmentation, reductionist approaches with their promise of a unified explanation seem highly desirable.

Whereas traditional philosophy of art takes artworks as a starting point, recent naturalistic approaches (e.g., Carroll, 2004) concentrate on the human cognitive faculties and behaviors that are responsible for the creation and enjoyment of these objects. After all, there is no experience of art except through our cognitive and perceptual systems. Thus, to understand why people create and enjoy art, it is important to understand its neurological underpinnings. Its universality across cultures also seems to warrant an explanation in biological terms. It is therefore not surprising that the first attempts to provide a unified explanation for art in biological terms date back to the 19th century. Experimental aesthetics (see Aiken, 1998, for an overview) was in fact among the earliest domains of experimental psychological investigation, with founders of the field like Wundt and Fechner probing their subjects' aesthetic responses to the golden ratio[2]. Later, Behaviorism was reflected in the experimental study of aesthetics. For example, Berlyne (1974) investigated the psychological basis of aesthetics as arising from the fundamental needs for arousal and excitement that are closely related to a drive for exploration and curiosity. Martindale's experimental analysis of patterns of stylistic change in European music (e.g., Martindale and Uemura, 1983) suggested that rapid stylistic changes do not stem from a universal drive to innovate, but rather from the human desire to avoid repetition and boredom. Martindale held the well-understood mechanism of habituation responsible for the craving for novelty in art in modern European and American culture.

Theoretical and conceptual developments in psychology, in particular the decline of Behaviorism and the growing influence of evolutionary theory in studies of human behavior are reflected in current scientific investigations of art. Evolutionary theory offers the possibility of a unified approach to human artistic behavior. Tinbergen's four questions (1963) form a useful starting point. Tinbergen (1963) proposed that any evolved trait or behavior can be explained through four complementary explanatory strategies: its proximate causal mechanisms (what physical structures, such as hormones or brain structures, are causally responsible for the trait), its ultimate function (how does the trait contribute to an organism's fitness, why did it evolve), its development (how does the trait

---

[2] The golden ratio is the relationship between two quantities, for example, the length and width of a rectangle, where the ratio of the sum of the quantities to the larger quantity is equal to the ratio of the larger quantity to the smaller one; it is approximately 1.618.

arise in individual ontogeny) and its phylogeny (its evolutionary history). This paper will focus on two of these questions: proximate and ultimate causes[3]. As we shall see, cognitive neuroscience primarily investigates proximate causal mechanisms (brain structures) responsible for artistic behavior, whereas evolutionary psychology mainly concentrates on ultimate causes (e.g., what are the consequences of artistic behavior for an individual's fitness). We will argue that the byproduct account of art, which conceptualizes artistic behavior as a byproduct of normal cognitive processes, rather than as an adaptation, is most successful in integrating these approaches. Given the current methodological and conceptual fragmentation in the field of art studies, such an integrative approach would be welcome.

Cognitive Neuroscience and Art

Cognitive neuroscience is a successful reductionist research program that provides causal accounts for cognitive states by reference to brain states. Subdisciplines like neuro-economics, neuro-ethics, or neuro-aesthetics attempt to provide neurally grounded explanations for phenomena typically investigated by the humanities, such as economic decision-making, moral judgments or aesthetic appreciation. By looking at patterns of brain activation (neuroimaging studies) and cognitive impairments following brain damage (lesion studies), it examines how the functional architecture of the brain produces cognitive processes. In this way, cognitive neuroscience seems well suited to address the proximate causal mechanisms that are involved in artistic behavior, in particular the brain structures that are responsible for art production and appreciation.

Since the brain is the only organ responsible for cognition, every cognitive task must yield a specific pattern of brain activation. Why then is it interesting to localize cognitive functions if all are localizable? If we put people who contemplate the Mona Lisa under a scanner, this will activate neural circuits dealing with face-recognition, emotion and perhaps theory of mind (our intuitive psychology that allows us to infer mental states, such as the reason why she might smile). It does not follow that the brain contains a "Mona Lisa module," even if these patterns of activation are stable across subjects. To constrain their research, neuroscientists look for *psychological primitives*, capacities that are not further reducible to other, more basic abilities. Due to these methodological constraints, they typically propose cognitive specializations at a relatively fine grain (Bechtel and Mundale, 1999). However, psychological primitives do not necessarily equate with single brain regions – rather, what is important is that the same areas are robustly activated across a wide variety of tasks (De Smedt, 2009). Theory of mind, for instance, activates a distributed network of neural circuits, including the medial prefrontal cortex, superior temporal sulcus, and temporal poles (Gallagher and Frith, 2003). What makes it a psychological primitive is that the same network is activated across a wide diversity of tasks that involve the attribution of mental states to others, such as beliefs and desires,

---

[3] For a discussion on the ontogeny of artistic behavior, see De Smedt and De Cruz (in press).

including interpreting cartoons and stories, or even watching simple geometric shapes "chasing" each other (Gallagher and Frith, 2003).

Does art constitute a psychological primitive? Neuroimaging studies of subjects looking at visual art indicate that propensities and biases of the visual system can account for many recurring features of art. Indeed, several authors (e.g., Latto, 1995) have argued that works of art capture our attention precisely because the artists that created them have unconsciously homed in on propensities of the human nervous system. For example, the search of artists like Mondriaan and Malevich for pure forms accords with the presence of orientation-selective cells in the primary visual cortex (V1) that respond selectively to dots and straight lines, especially to horizontal and vertical ones (Zeki, 1998). This is part of the earliest stages of processing by our visual system. Mondriaan's *Trafalgar square* (ca. 1943) is a typical example of visual art that stirs the orientation-selective neurons in V1. Since the Late Pleistocene, combinations of straight lines are commonly found, for instance in the engraved ochre plaquettes from Blombos cave, South Africa (about 75,000 years old), as are dots on Franco-Cantabrian cave walls (e.g., the spotted horses from Pech Merle, France, 16,000 years old). Such designs are also observed on artifacts from diverse periods (e.g., decorative lines and dots on earthenware from the Linear Pottery culture from the European Neolithic, 5500-4500 BC) and in the artistic production of many nonwestern cultures (e.g., geometric patterns on basketry or cloth). The pervasiveness of geometric designs across widely divergent cultures and periods may be explained by the fact that they are appealing to the early human visual system (Hodgson, 2006). Although the popularity of geometric designs could also be due to the fact that they are simple to render, and that they can be used as building blocks of more complex designs, as in Yuan and Ming dynasty Chinese painting, where bamboo is rendered with a few simple brush strokes, the fact that they are consistently used alongside more complex designs (e.g., dot and stripe patterns alongside animals depicted in Paleolithic imagery) provides evidence for their intrinsic appeal.

Some forms of art key in on trichromatic color processing, a visual system humans have in common with most diurnal primates. Color-sensitive cells in the visual areas V1 and V2 are mainly concerned with registering the intensity and presence of color fields. Artists like Rothko or Klein produced paintings with large iridescent color fields that key in on this stage of color processing (Zeki, 1999, p. 189). By contrast, fauvist and expressionist canvases evoke responses in V4 and in the inferior temporal and frontal cortices (Zeki and Marini, 1998), which are involved in matching colors to objects. People process images with correct colors in a different way from images that have colors that are not commonly associated with the objects they depict, such as blue strawberries. The latter elicit a strong activation of the dorsolateral frontal cortex (Zeki and Marini, 1998). The unusual neural pathways associated with our perception of mismatching colors may provide an explanation for why such images are attention grabbing. Fauvist and expressionist painters unknowingly hit upon this when they began to paint objects in mismatching colors, like Matisse's portraits of his wife, with green and blue patches across her face, or the blue horses by Marc.

Yet other forms of art are experimentally associated with an increased activation in the motion-sensitive visual areas, such as the medial temporal and medial superior temporal cortices (Zeki, 1998). This is not only the case for dance, but also for contemporary art forms like mobiles by Tinguely and Calder. A Positron Emission Tomography study (Brown, Martinez, and Parsons, 2006) of subjects who tango revealed that dance involves a network of neural circuits normally engaged in ordinary bipedal locomotion and in the organization of complex sequences of movements. Somewhat surprisingly, the activation of the medial temporal and superior temporal cortex is also observed in subjects who look at classical and renaissance sculptures in *contrapposto* stance[4] (Di Dio, Macaluso, and Rizzolatti, 2007). Apparently, brain areas that visually analyze motion are not just active when seeing actual motion, but also when it is implied.

Music, too, recruits brain mechanisms that are associated with a variety of normal, everyday cognitive activities. Listening to music recruits Broca's area and the orbitalis region of the left inferior frontal cortex, neural regions specialized in the processing of grammatical structure (Levitin and Menon, 2003). Music that violates expectations in rhythms or harmonic structures activates brain areas that were previously implicated in violations of syntax in language (Maess, Koelsch, Gunter, and Friederici, 2001). At the same time, experimental evidence (e.g., Huron, 2004) indicates that people who listen to music have a clear preference for expected over unexpected sounds, and find the former more pleasant. Many musical devices, such as the *appoggiatura* (an embellishment along the main note) or harmonic cadences (the use of at least two chords to conclude a section or phrase of music) promote prediction by the listener (Huron, 2004). Classical period compositions, for instance by Haydn or Mozart, often balance on a cognitive optimum between predictability and violation of expectation: They are predictable enough to evoke pleasurable responses, but occasionally violate these predictions so that the audience remains interested and focused, for example by inserting changes in modulation and rhythm, introducing elements from folk music, or by incorporating unusual instruments (e.g., Leopold Mozart's *Cassation in G for toys, two oboes, two horns, strings and continuo*, that introduces toy instruments into an otherwise normal orchestral piece). Because neuroimaging studies rely on stimuli of limited duration, at present no such studies have probed what neural mechanisms underlie the perception and appreciation of literature. It seems, however, that short stories and jokes invoke neural circuits involved with theory of mind (Gallagher and Frith, 2003) – presumably, the same would be true for someone reading Tolstoy's *Anna Karenina* (1878[1995]).

An interesting pattern emerges from these studies on different types of art: In all cases, the aesthetic responses are elicited by tapping into the normal functions of perceptual systems in unconventional ways. Why should the perception of blue horses, which yields an enhanced response in the inferior temporal cortex, or of atypical musical structures, leading to an increased activity in Broca's area, elicit aesthetic responses? Given the limited attentional resources of the brain, perceptual inputs compete for neural space. It thus seems likely that because of their importance to the survival and reproduction of an organism, some cues are given priority by the early perceptual systems – for example, as we shall see further on, the human auditory system is especially well attuned to the acoustic

---

[4] Contrapposto is a term for a dynamical position of a human figure, where its weight is shifted onto one foot (a well-known example is Michelangelo's *David*).

properties of the human voice, and the human visual system is apt at recognizing face-like stimuli. The brain could be regarded as a set of world-interpreting mechanisms that lead us to ignore some aspects of the world, while others are accorded disproportionate attention. Aesthetic responses may find their origin in the brain's reward system, which guides attention to relevant perceptual input (Barry, 2006). Ramachandran and Hirstein (1999) propose that successful art exploits these tendencies, thereby eliciting strong emotional responses. Some cognitive neuroscientific studies provide support for these views. Looking at paintings one deems beautiful activates reward-based emotional circuits compared to duller paintings (Vartanian and Goel, 2004). Similarly, participants looking at canonical classical and renaissance sculptures show higher activation in the anterior right insula compared to a control condition in which the proportions of these sculptures have been digitally altered so as to look less harmonious (Di Dio et al., 2007). The anterior right insula is a part of the limbic system that is consistently involved in mediating cravings for food and so-called recreational drugs and in providing an emotionally relevant context for perceptual experience (Garavan, 2010). Likewise, people listening to their favorite music show stronger activation in reward and motivation-related brain areas compared to control compositions (Blood and Zatorre, 2001).

This intimate connection between the function of art and the function of the brain led Zeki (1999, p. 10) to quip that artists are in a sense neuroscientists, since art, in order to be successful, must appeal to human perceptual, conceptual and motivational systems. In other words, art appeals to us because it exaggerates or appropriates features that human perception is tuned to (e.g., faces, color contrasts) while ignoring or underplaying other features that are less important to human perception. For example, many works of visual art contain revealing systematic mistakes in rendering perspective, shadows, and reflections accurately. Take shadows as an illustration. Painters typically do not depict shadows realistically. Outside of western art, most traditions omit shadows altogether (Gombrich, 1995). When artists do attempt to paint shadows, they often fail to do this consistently: An examination of a corpus of western historical paintings (Casati, 2008) revealed that painters tended to produce a replica of the visible profile of the caster when depicting shadows, which yields impossible shadows (e.g., the correct shadow of a cube would look trapezoid or rectangular, but painters instead just make an outline of the cube in grayscale). Most observers are not bothered by these inconsistencies in lighting – indeed, without being told about them, they do not even notice them (Cavanagh, 2005). In accordance with this, developmental psychological studies indicate that an understanding of the behavior of shadows only emerges in late childhood. Infants, for example, show no surprise when a shadow behaves anomalously with respect to the object by which it is cast (Van De Walle, Rubenstein, and Spelke, 1998). Even adults have difficulties predicting what shadows will look like given the distance and angle of a light source and the shape of an object (Ostrovsky, Cavanagh, and Pawan, 2005). Shadows have been put to dramatic use in film noir and expressionist movies such as in Murnau's 1922 horror movie *Nosferatu, eine Symphonie des Grauens*, yet even there the actual shape of the shadows has been distorted beyond what would normally be cast by the actors, something that does not seem to bother the audience.

The intimate fit between artistic production and human cognition can explain why artists are unconsciously drawn to some art forms over others, or when, if a new artistic style is developed, it tends to evolve in specific ways. Take the example of abstract art: Since the 18th century, artists have attempted to break free of aesthetic conventions in order to capture the essence of their subject matter, culminating in abstract art. Yet, as we have seen, abstract art often appeals strongly to early perceptual systems, by using vivid colors, straight lines or sharp contrasts, exploiting amongst others areas V1, V2 and V4. The perceptual tendencies of the human brain can be seen as cognitive attractors that have channeled abstract art in preordained directions, in particular, a tendency toward more clear-cut, simplified and geometric shapes, brighter colors and higher color contrasts, arguably because these features elicit stronger responses in the artist's and viewer's early perceptual systems. In the work of well-known artists like Klee, Mondriaan and Matisse, one can indeed observe an evolution toward the progressive influence of these cognitive attractors, in the increasing use of strong lines, vivid colors and bold contrasts. Ironically, by striving to escape from artistic conventions, abstract artists were lured into the conventions of the human perceptual systems. Or, to put it more positively, as "to abstract" means "going back to the essentials," abstract art has indeed succeeded in stripping away cultural conventions by reverting to elementary responses of the human perceptual systems.

Taken together, neuroimaging studies suggest that art is not a psychological primitive. Rather, it hijacks the preferences of normal perceptual and motivational neural circuits. Lesion studies provide an equally compelling case: Art production seems to continue irrespective of the location or extent of the lesions in the brain of the artist. Not even at the very rough level of hemispheric specialization do we see any modularity in artistic behavior – the loss of function in either hemisphere does not automatically lead to an inability to create art (Zaidel, 2005). In a case study of an Asian-American artist, Mell, Howard and Miller (2003) document the gradual shift over 12 years from conventional Chinese themes to a bolder, expressionist style throughout her cognitive decline due to fronto-temporal dementia (FTD). Remarkably, some patterns of brain damage, resulting from FTD, are correlated with an emergence of artistic skills in previously non-artistic individuals (e.g., Miller et al., 1998). The five patients (all in their 50s or 60s) described by Miller et al. (1998) all spontaneously began to take up art classes, painted, sculpted or photographed obsessively without any previous interest in art, and were later diagnosed with FTD. Their interest in art is thus not a result of therapy. FTD patients typically have impairments in language, executive control and social skills, but remain relatively unaffected in the domains of visual perception and motor skills. According to Miller et al. (1998), the decline in inhibitory control that is typical for FTD might facilitate the already present capacities for visual art production in these subjects. Alternatively, the patients may have chosen to focus on visual art because of the difficulties they experienced in other domains, such as social interaction, and the relative preservation of their motor and visual skills. In either way, this research suggests that the capacity to make art is not restricted to the select few, but is present in the population at large. This may also be true for music. A study that investigated musical memory (Racette and Peretz, 2007) suggests that professional musicians are not significantly better than laypeople in recalling the melody, rhythm and lyrics of unfamiliar folk songs, despite their extensive training in and familiarity with music.

If art is not a psychological primitive but an epiphenomenon, cognitive neuroscience cannot study art as such – indeed, what the neuroscience studies seem to tell us is that when subjects view a work of art, they do not see, say, a canvas or a statue; rather, they react to what it represents (e.g., a seascape, a nude woman). However, cognitive neuroscientists who examine artistic behavior (e.g., Vartanian and Goel, 2004; Zeki, 1998) do not claim that art does not correspond to anything in the real world. Quite on the contrary, many of them (e.g., Cavanagh, 2005) argue that the history of art can inform theories of the human mind, because successful art provides a window onto invariant properties of the human perceptual systems.

Art as Adaptation

Evolutionary psychology aims to explain features of human behavior as a product of an interaction between evolved psychological mechanisms and the environment, making use of methods from evolutionary biology, such as kin selection or parental investment theory. It does not regard culture as completely autonomous but as at least in part reducible to the human evolved cognitive architecture. Evolutionary psychologists disagree about the extent to which this reduction of culture to evolved cognitive tendencies is possible. Some (e.g., Tooby and Cosmides, 1992) argue that most of culture consists of "evoked" cognitive predispositions, while others (e.g., Dunbar and Barrett, 2007) allow for a larger influence of culturally transmitted norms and rules in governing human behavior. Nonetheless, much of the evolutionary psychological literature is clearly unificationist, as it attempts to "integrate the social sciences into a seamless system of interconnected knowledge that runs from astronomy to biology" (Tooby and Cosmides, 1992, p. 19).

Some evolutionary psychologists (e.g., Barrett and Kurzban, 2006), like the majority of cognitive neuroscientists, are also committed to a model of functional specialization in human cognition. In contrast to cognitive neuroscientists, this functional specialization is not cast in anatomical terms, but in terms of evolutionary theory: The mind contains domain-specific computational devices that deal with problems our ancestors recurrently faced. Typically, the cognitive adaptations that evolutionary psychologists propose are less fine-grained than the psychological primitives studied by cognitive neuroscience, corresponding to real-world adaptive problems like cheater detection or the attribution of mental states. The evolutionary rationale for this is that different adaptive problems can be solved more efficiently by specialized mental subsystems than by a single holistic processor. Even without this commitment to adaptationism, an evolutionary approach does seem to favor some form of functional cognitive specialization, because many computational problems (e.g., mate selection and foraging) are functionally incompatible (the criteria for choosing a mate are different from those for finding food) and thus cannot be adequately handled by a single computational device (Cosmides and Tooby, 1994).

Although evolutionary psychologists are interested in both proximate and ultimate explanations in a variety of domains of human behavior, their examinations of art have so far concentrated on ultimate explanations of why people spend considerable time and energy in their production and enjoyment of art. Two types of approaches to explaining artistic behavior have been proposed: either that it is an adaptation, which has evolved in direct response to one or more selective pressures in our ancestral past, or that it is a byproduct of other adaptations that does not serve an adaptive function in itself. Its complexity makes it implausible that art would have evolved through random genetic drift.

Those (e.g., Dissanayake, 2000) who favor the view that art is an adaptation invoke its universality across cultures, its costliness in terms of time and energy, and its early and spontaneous development in children. We will briefly discuss a selection of recent adaptationist models for art. Miller (2000) argues that art and other forms of human creative behavior evolved as a result of sexual selection: Their costliness in terms of time and energy provided ancestral hominids with an honest signal of the fitness of the art-producing person (in Miller's view, primarily the art-producing male). Just like a lush but burdensome tail in peacocks or birds of paradise is a good signal of its owner's qualities to live with such a handicap, the artworks honestly signal the artist's qualities as a mate. In support of his hypothesis, Miller (1999) shows that the artistic production of western male writers, jazz musicians, and painters peaks during prime reproductive age, with a higher productivity in quantitative terms compared to their female peers. The latter have a more even distribution of artistic output across their lifespan, and do not experience the sharp decline in artistic production during middle age that is typical of their male fellows. A potential problem with this evidence is that it is solely based on an analysis of western artists. The quantitatively higher male output may be due to socio-cultural factors, such as gender-based prejudices in perception of male versus female artistic qualities. A way to control for this possible western bias would be to replicate Miller's study in nonwestern cultures, especially in those where women are responsible for a substantial part of the art production. For example, in Tonga (a Polynesian kingdom), woven ceremonial mats that are exclusively the work of women have high aesthetic and cultural value – a collection of such mats constitutes the Tongan crown jewels (St. Cartmail, 1997). These ceremonial mats are not primarily functional objects (although they resemble functional, non-decorated mats in some respects) and are thus a good analogy to the (primarily non-functional) art production in western culture. Tongan men, on the other hand, carve functional wooden objects like decorated bowls and neck supports. A cross-cultural test of Miller's hypothesis evaluating art production in cultures where both men and women are active artists (such as Tonga, or Navajo native Americans) could examine whether men still have a higher quantitative production in these cultures, and whether there is a correlation in men (but not in women) between a peak in artistic production and the prime reproductive years. Even if this were the case, there is yet another possible confound to Miller's hypothesis, namely more general sexual differences in motivation and drive: Men might be more prone to have a high quantitative output of art for the same reason that they seek higher income jobs. Indeed, Kanazawa (2000) found that male but not female scientists tend to write the lion's share of their papers in their prime reproductive period. Thus, sexual differences in art production could be the result of sexual selection, but this does not entail that sexual selection specifically targeted art and other cultural displays.

Tooby and Cosmides (2001) point out that pretend play emerges universally in toddlers. This ability provides us with the imagined worlds of (oral and written) literature and visual art, risk-free environments where learning can take place through vicarious experience: Fairy tales like Snow White tell of the competition that may arise between fading mothers and nubile daughters, whereas novels like Austen's *Sense and Sensibility* (1811[1986]) provide an insight into human mate selection dogged by financial worries. Although this hypothesis sounds intuitively plausible, it has not been empirically investigated. A possible test for Tooby and Cosmides' (2001) claim might be to investigate correlations between early exposure to fiction and performance in theory of mind tasks. Some studies (e.g., Taylor and Carlsen, 1997) indicate that children who engage more in imaginative play (i.e., creating fictional environments) are advanced in theory of mind comprehension compared to their less imaginative peers. Future work may indicate to what extent being engaged in fiction (such as children's books, read aloud by parents) has an effect on the developing theory of mind.

Dissanayake (2000) proposes that art is the intentional act of making everyday behavior special through exaggeration, formalization, or manipulation of expectations: dance exaggerates and formalizes normal bodily movements; songs distort normal speech and prosody. Performing such actions together relieves tension and anxiety, thus improving social bonds within the community: Such rituals "build and reinforce feelings of unity among adults, all of which ultimately serve to hold the group together" (Dissanayake, 2000, p. 64). She traces the evolutionary precursor of these behaviors to mother-infant dyadic interactions, where mothers and infants spontaneously engage in intentionally modifying their vocalizations, gestures and facial expressions. One potential source of tension in this account is that it has conflicting notions on the level at which selection operates. On the one hand, Dissanayake seems to favor a group selectionist account of art, as she identifies fitness benefits of art at the group level, such as an increased cohesion between group members (e.g., Dissanayake, 2000, pp. 64, 168). On the other hand, she has emphasized that art is a result of individual selection, since, according to her, "Art is a behavior potentially available to everyone because all humans have the disposition to do it" (Dissanayake, 1995, pp. 34–35). To Dissanayake, this indicates that art is the result of selection at the individual level: "Art-inclined individuals, those who possessed this behavior of art, survived better than those who did not. That is to say, a behavior of art had 'selective' or 'survival' value" (Dissanayake, 1995, p. 35). Unfortunately, the claim that art improves survival chances has not been experimentally tested. Furthermore, insisting that a selectionist account needs to operate at the individual level requires more backing up: Cross-cultural research (e.g., Anderson, 1989) indicates that the production of art by adults is usually the work of specialists. As Davies (2005, p. 295) pointed out, Dissanayake could have opted for a weaker position, where only a few talented persons make art, but where art is still a pan-cultural phenomenon. As long as a sufficient number of individuals make art, the adaptive benefits of art could be available at group level. Indeed, mathematical models of cultural group selection can be applied to the evolution of particular artistic traditions, such as the development of portable art (so-called Venus figurines) in Ice Age Europe (De Smedt and De Cruz, in press).

For art to be an adaptation, it does not suffice to come up with the observation that art serves adaptive functions in some context. Adaptationist explanations for art need to specify what it is an adaptation for. Clearly, it is not difficult to come up with adaptive functions for art, but that is exactly the problem of such adaptationist accounts. It remains as yet unclear what selective pressures may have promoted the emergence of art in the Late Pleistocene, therefore theorizing about it remains fairly unconstrained. The current selective benefits of art (for example, in terms of sexual selection) are not necessarily the same as those in the past. It is interesting to note that most adaptationist approaches to art are concerned mainly with literature (see, e.g., the papers collected in Gottschall and Wilson, 2005), where the function of vicarious learning is quite plausibly explained. However, it remains unclear to what extent such an approach can be generalized to other arts, especially abstract art, music and dance. Those approaches that sketch a theory that encompasses most arts have the problem that the category of objects that is being explained is wider than what we normally regard as art. Miller (2000) explains not only art, but also humor and even conspicuous consumption (the wasteful advertising of one's resources by spending them on luxury items or giving them away). Tooby and Cosmides (2001) themselves point out that their adaptive account is about fiction, the broad human ability to imagine counterfactual worlds and situations. Dissanayake (1995, 2000) provides not only an explanation for art but also for ritual and ritualized behavior, which is not even restricted to humans, but can be observed in many animals living in captivity and perhaps also in the wild (see Bekoff, 2009, for a tantalizing report about grieving magpies). To date, no adaptationist explanation makes a plausible case that targets artistic behavior in its entirety.

Art as Byproduct

Some evolutionary psychologists explain art as a byproduct of the evolved human mind, without the further claim that it is an adaptation. For instance, to Pinker (1997), art's primary function is not to increase our biological fitness, but to "press our pleasure buttons" (pp. 514-525). For Pinker, art exploits aesthetic preferences that were (or are) adaptive in other contexts, just like cheesecake gratifies our craving for sugar and fat.

A potentially fruitful domain of investigation for byproduct explanations of art is the study of cross-culturally stable properties of artistic production. The cross-cultural prevalence of some forms of art can be explained by their efficiency to exploit our evolved cognitive predispositions. Although human creativity can in principle create a wide diversity of artistic expressions, some of these will enjoy more success and have a higher chance to be incorporated in artistic traditions because of their fit with our cognitive biases. In the domain of music, scales provide an interesting example. Scales are collections of tones that divide octaves into specific intervals. Since humans can discriminate between about 240 pitches over an octave in the mid-range of hearing (Fastl and Zwicker, 2007), in principle a very large number of scales are possible. Yet, in practice, musical traditions only explore a modest subset of these possibilities: most scales across time and cultures are only between five and seven tones, often with well-defined intervals between them. Gill and Purves (2009) argue that this conformity can be explained by the fact that pentatonic and heptatonic scales (*natural* scales, not well-tempered scales as in modern western music) are close to harmonic series, which find their origin in the way humans perceive speech. Human vocal fold vibrations characteristic of voiced speech are mathematically best described by harmonic series. These function as cognitive attractors: The cross-cultural preference of a very limited number of scales may be explained by their fit with the evolved human auditory system, which is tuned to harmonic series. Gill and Purves (2009) demonstrated that scales that are widely used cross-culturally, like the minor pentatonic scale (as in *Mary had a little lamb*) and the Phrygian heptatonic mode (e.g., Ralph Vaughan Williams' *Fantasia on a theme of Thomas Tallis*), indeed correspond closely to harmonic series, whereas scales that are only rarely used across cultures, such as the Locrian mode (for instance, Metallica's *Sad but true*), bear the least resemblance to them. An external confirmation of this hypothesis is the sound produced by a reconstruction of a 36,000-year-old flute made of swan bone from Geißenklösterle, southwestern Germany, by the experimental archaeologist Friedrich Seeberger. The flute produces four tones and three overtones that fall neatly into a minor pentatonic scale. Seeberger (2003) can be heard playing the flute on a CD. The minor pentatonic scale is the most widely used musical scale cross-culturally, and it is also the scale that is closest to harmonic series. Next to this, most music, even purely instrumental music, is composed within the human vocal range, indicating that music may be based to some extent on auditory adaptations involved in human speech perception. A recent study with cotton-top tamarins (Snowdon and Teie, 2010) provides indirect support for this hypothesis. The monkeys did not exhibit any noticeable behavioral reactions to human music, compared to a baseline control condition in which no music was played, which the experimenters interpreted as indifference. By contrast, the animals responded strongly to cello compositions that were modeled on tamarin vocalizations, showing arousal when they heard music based on aggressive vocalizations, and decreased activity and calm behavior when they listened to melodies based on affiliative calls. Human subjects found neither of the tamarin-vocalization based compositions pleasant. Although music is more than a rendition of vocalizations, these studies indicate its species-specificity.

Conversely, some authors (e.g., Hauser and McDermott, 2003) argue that music depends on ancient auditory properties that predate the evolution of language. The salience of some tonal intervals in musical scales may be based on auditory sensitivities that humans share with other primates. There is some experimental support for this. Rhesus monkeys, manifestly a species that does not produce music, can correctly identify two versions of the same short tonal melody as the same, for example, when one version is played an octave higher. Interestingly, like with humans, their performance drops sharply when they have to identify atonal melodies (Wright, Rivera, Hulse, Shyan, and Neiworth, 2000). However, in other respects, human musical ability is more akin to that of distantly related clades, such as songbirds and cetaceans, than to that of our closest living relatives, the nonhuman apes. Whereas songbirds and cetaceans learn songs through social transmission (e.g., Foote et al., 2006), apes, with the exception of gibbons, do not produce anything akin to song (Geissman, 2000) – and gibbon song does not depend on transmission through learning but is stereotypical and species-specific: A hybrid of two species of gibbon will combine songs of both parents, even if it was only exposed to the song type of one of the parents (Geissman, 2000, pp. 108-110). Despite many efforts, no nonhuman ape has mastered the ability to learn complex, novel vocalizations through social transmission (Fitch, 2005). Taken together, the limited evidence for musical ability and recognition in primates indicates that music may be specific to humans within the primates, and that it draws to an important extent on adaptations that are involved in the production of voiced speech, including vocal fold vibrations and grammar, which evolved after hominids split from other ape lineages.

In the domain of visual art, we can also expect that visual stimuli that are significant from an evolutionary perspective will feature prominently in art production. The canvases by Komar and Melamid indicate that the taste of naive art observers may be guided by more than cultural influences. These paintings, based on polls that probed aesthetic preferences in different countries, are remarkably stable across cultures: They invariably feature tranquil landscapes around a lake with relaxing humans in the foreground and some large animals in the distance (readers can visit http://www.diacenter.org/km/ for a flavor of this work). This is in line with studies (e.g., Orians and Heerwagen, 1992) that reveal a universal preference for semi-open savannah-like landscapes with trees and water, reminiscent of the environment in which a large part of hominid evolution took place.

Another example is face perception. Newborns can already discriminate faces from other objects by detecting the shadowy patches created by eyes and mouth (Farroni et al., 2005). Face-recognition is a highly specialized capacity in humans and other primates. Its neural basis is the fusiform face area, a part of the cerebral cortex that is specialized in the processing of face-like stimuli, and that has characteristic features, such as a diminished ability to recognize inverted faces (Pascalis and Bachevalier, 1998). Face recognition probably evolved as a means to visually recognize conspecifics, as diurnal primates have less developed olfactory capacities compared to other mammals, and therefore cannot easily recognize each other by smell. A considerable part of the world's art production (e.g., portraits, busts, and masks) keys in on this evolved face-recognition system. Interestingly, some studies tentatively suggest that cultural face-like stimuli emphasize those parts of the face that humans find especially salient. Infants pay most attention to the eyes and mouth, and less to features like eyelashes or cheeks (Farroni et al., 2005). Still, face-like stimuli that are very schematic (such as smileys) elicit less neural response in the fusiform face area than realistic faces (Tong, Nakayama, Moscovitch, Weinrib, and Kanwisher, 2000). One could predict on the basis of this that successful cultural face-like stimuli will have some degree of realism, but that they nevertheless emphasize the eyes and mouth. In support of this, Costa and Corazza (2006) found that realistic self-portraits and likenesses drawn from memory by art students show significant increases in the size of the eyes and the lips. The effect is also discernible in historical portrait art, such as in the striking Fayum mortuary portraits. Future research can elucidate how cognition and culture interact, for example, in the cultural evolution of face-like stimuli such as portraits or masks within particular traditions. An fMRI study of one novice and one expert portrait artist, who were asked to draw a series of faces (Solso, 2000), revealed an increased activity in the fusiform face area in both participants (albeit somewhat less in the expert) compared to a control condition (drawing geometric figures), indicating the importance of this area for the production and perception of face-like stimuli. The lower activation in the expert's brain might be a consequence of more efficient processing of faces, a result of extensive training and practice. However, since both subjects were allowed to look at the faces and their own drawings during the production task, it is unclear whether this activation is merely due to visual perception, production or both. Miall, Gowen, and Tchalenko (2009) asked untrained participants to draw cartoon faces from memory, preventing them from looking at their own hand or drawings during the task, thereby controlling for visual perception versus production of face-like stimuli. Their fMRI study indicated that drawing cartoon faces without direct visual perceptual input indeed also activates the fusiform face area.

Equally striking is the prevalence of animal imagery in visual art across the world, from the early Upper Paleolithic on. Indeed, the earliest representational art depicts almost exclusively animals. Large dangerous carnivores and large and medium game figure prominently among the mammoth ivory figurines of about 36,000 years old, excavated in southwestern Germany (Conard, 2003) and among the slightly younger cave paintings of the Grotte Chauvet in southern France (Feruglio, 2006). Even in industrialized countries, where contact with animals is relatively sparse, depictions of animals have not diminished in popularity – unsystematic observations by parents and teachers indicate that the drawings by young western children teem with quadrupeds, birds and fish. The salience of such imagery may be explained by the priority our perceptual systems give to animal shapes. New, Cosmides, and Tooby (2007) demonstrated that subjects are substantially faster and more accurate at detecting changes in complex scenery when animals (even small ones like pigeons) were introduced or omitted compared to inanimate objects, even vehicles, which they have been trained for years to monitor for sudden life-or-death situations in traffic. As this efficiency could not be accounted for by differences in lower-level visual characteristics or expertise, the authors assumed that people might have an advantage in animal categorization by virtue of the ancestral importance of this ability, regardless of its current utility. After all, hominids have been active hunters for at least one million years (Rabinovich, Gaudzinski-Windheuser, and Goren-Inbar, 2008) and had to be aware of predators and venomous animals for a much longer period. Neuroimaging studies (e.g., Caramazza and Mahon, 2003) suggest that some parts of the temporal and occipital cortex are exclusively dedicated to perceiving and thinking about animals. Remarkably, the neural correlates that correspond to the perception of animals are similar in sighted people as in congenitally blind subjects (Mahon, Anzelloti, Schwarzbach, Zampini, and Caramazza, 2009), indicating that this neural organization is not the result of perceptual features of animals, but rather of selective pressures that have formed specialized areas within the human brain that deal with semantic knowledge about animals. More systematic empirical research could examine to what extent art that has animal imagery or themes is influenced by evolved cognitive predispositions. For example, recent studies (e.g., Allen, Bloom, and Hodgson, 2010) indicate that young children have a preference for animal imagery that is canonical (e.g., elephants shown in profile, rather than in frontal view) and rich in relevant detail. Taken together, this leads to the following prediction: Art that depicts animals will tend to represent those kinds of animals that humans interacted with (prey animals, predators), regardless of their current effect on human fitness – it will rather show large carnivores than malaria-carrying mosquitoes, even though the latter have currently more impact on human fitness. Some artistic traditions, like Upper Paleolithic animal imagery in sculptures and cave paintings indeed seem to conform to this, showing high frequencies of predator and prey animals in prototypical postures. More systematic work is needed to examine to what extent this is also the case for more recent animal imagery in figurative art in western and nonwestern cultures.

If we take consilience, the convergence of two or more independent scientific disciplines, as a useful scientific heuristic, the byproduct account of art is preferable to the adaptationist view, because the former is more in line with cognitive neuroscience. The cognitive neuroscientific evidence reviewed here provides strong empirical support for the claim that various forms of art, including visual art and music, are attention-grabbing because of their correspondence with evolved propensities of the human neural system. The most likely proximate explanation for why masks, for example, elicit attention is that they activate the fusiform face area. The functional specialization of face-detection is such that perceiving faces is ineluctable: We cannot look at a depiction of a face and choose to regard it as a meaningless configuration of colors. A visual stimulus that has the main features of a face, such as a portrait or mask, thus compels the brain to pay close attention to it. The ultimate reason for the cultural success of masks and portraits around the world can be found in the evolutionary salience of face detection for humans – highly social animals that put a premium on individual recognition.

It is important to note that artists need not be consciously aware of this effect. Artists generally do not know the effects their work has on the neural activity of their audience. Random variations in artistic style can be cumulatively retained to the effect that specific artistic traditions come to correspond more closely to evolved cognitive predispositions as a form of cultural selection. We already mentioned the tendency of early 20^{th}-century abstract art to emphasize bright color contrasts and lines, and the cross-cultural prevalence of musical scales that correspond to harmonic series. A short historical example can further clarify how this unconscious selection of artistic variations may be one of the driving forces in the cultural evolution of artistic traditions, next to culture-specific norms and preferences. Koops (1996) examined the physical appearance of children depicted in Dutch and Flemish paintings from the 15^{th} to the 20^{th} century. He drew on Lorenz's (1943) theory of the "child schema" (*Kindchenschema*), which proposes that specific anatomical proportions of the face and body (in particular, a relatively large head, high forehead, large eyes, and short and thick limbs) elicit nurturing behavior and affective responses. In the Middle Ages, babies and children were depicted as miniature versions of adults. From the 17^{th} century onward, infants, children and even adolescents look progressively more neotenous (i.e., childlike). In other words, more recent paintings turn out to correlate more closely with the child schema, perhaps because Dutch and Flemish painters and their patrons found neotenous children more attractive. It is not that visual preferences changed; the preference for neoteny is probably a stable feature of adult cognition. Rather, this feature may have played a role as a selective pressure to retain small variations in depiction of children and infants. Paintings with infants and children that had slightly larger eyes and slightly higher foreheads were more successful than those with smaller eyes and lower foreheads, pushing the design of these portraits in the direction of babylike faces. The increasing chubbiness cannot be solely explained as a result of a better diet, since this long period (15^{th} to 20^{th} century) was punctuated by famines. It is also unlikely that the increased neoteny in depicted infants and children was solely driven by concerns for realistic depiction, as late medieval painters like Van Der Weyden or Van Der Goes could paint very realistic-looking adults, animals and plants, while the infants they painted looked like tiny adults. Moreover, exaggerated neoteny is observed in other cultural stimuli, such as the increasing childlike appearance of teddy bears in the course of the 20th century which display increasingly higher foreheads and shorter snouts (Hinde and Barden, 1985). More recent examples of neoteny include toys like Littlest Pet Shop and My Little Pony, where there is a similar increasing size of eyes and head, accompanied with a progressive shortening of snouts and limbs. Interestingly, Morris, Reddy, and Bunting (1995) found that this cultural evolution in toys was not driven by the consumers (the children) but by their parents, who buy the toys and are thus the selecting agents. The ultimate explanation for why humans prefer cuteness in cultural stimuli is the fitness benefit it conferred to ancestral parents who were compelled to nurturing and caring for individuals whose features corresponded to the child schema. It remains a topic of future research, however, to identify the primary selective agent in the evolution of art: the preferences of the artists, or of the patrons or purchasers, or of both?

The evolutionary psychological byproduct account of art provides a satisfying explanation for the cross-cultural human drive to create and enjoy art, and for the recurrence of some forms of art (e.g., musical scales, faces, animals) across time and cultures. The evolutionary byproduct explanation and cognitive neuroscientific account strengthen each other. However, a few questions remain unanswered. The byproduct account does not explain why we do not invariably prefer art that maximally conforms to evolved cognitive mechanisms. Academic art[5] by painters like Bouguereau or Fragonard generally responds to our evolved tastes in depicting attractive men and women in lush landscapes. Yet some influential art critics (e.g., Greenberg, 1991, p. 32) derisively refer to this type of art as overpolished and clichéd. Many highly acclaimed works of visual art are hardly eye candy, such as Goya's gloomy political canvases or Bacon's haunting papal portraits. Unsurprisingly and in accordance with the folk concept of art, untrained art observers do prefer academic painters like Alma Tadema or Bouguereau (Martindale, 1998), probably because their works are more in agreement with our evolved cognitive tendencies. Nevertheless, the fact that this preference for such artistic forms is not universal remains unexplained.

Another future challenge for the empirical study of art consists of individual differences in art perception and production. What makes some people more prone to create art? What distinguishes art critics from the general public? Cross-culturally some people are more drawn to art production than others. Even relatively egalitarian societies have artists (i.e., individuals that are regarded as especially competent in sculpting, storytelling, or dancing by members of their community; Anderson, 1989). An adaptationist perspective, such as the one advocated by Miller (2000), can explain such individual differences as a result of frequency-dependent selection. Indeed, empirical tests that examine the relationship between artistic creativity, schizotypy and reproductive success indicate that an increased reproductive success associated with artistic capacity may be offset by the prevalence of traits indicative of schizotypy (which reduces fitness) in British poets and visual artists (Nettle and Clegg, 2006). This does not exclude an explanation of individual

---

[5] "Academic art" denotes paintings and sculptures in a style that was taught at European academies of the arts, mainly during the 18th and 19th century.

differences in artistic capacities under a byproduct account. If art is a byproduct of evolved cognitive capacities, we may expect that a combination of individual differences in these capacities, and personal interest and circumstance may explain why some become artists, whereas others do not. Indeed, such models have been developed for other capacities that are seen as byproducts of evolved abilities, such as mathematical reasoning skills (e.g., Geary, 1995). Like art, these skills are the result of a co-optation of abilities that have an unrelated evolutionary function, and they are sensitive to cultural context.

Do Reductionist Approaches Obviate the Need for Higher-level Accounts of Art?

Cognitive neuroscientific and evolutionary psychological approaches can help us understand the cognitive processes that underlie art. From this examination of both approaches, a coherent picture emerges of art as a byproduct of normal perceptual, motivational and emotional brain circuits that have evolved in response to problems originally unrelated to art. However, from neither discipline does it become clear that art should be a meaningful subject of investigation within their explanatory frameworks. As discussed earlier, several cognitive neuroscientists (e.g., Barry, 2006; Ramachandran and Hirstein, 1999) argue that art draws on perceptual and motivational neural structures involved in everyday experience. As we have seen, evolutionary psychologists who propose adaptationist accounts for art (e.g., Dissanayake, 1995; Miller, 2000) typically target a category of behaviors that is broader than art (e.g., cultural display). Byproduct explanations too, do not consider art as a natural category: They make no distinction between an artwork and perfume, cheesecake or pornography, since all these exploit our evolved perceptual biases. The humanities, such as aesthetics and art theory, can investigate aspects of art that are not reducible to universal features of human psychology, but that are variable across time and cultures. Arguably, the striking dissimilarities in the way human figures are rendered in Utamaro's or Hokusai's woodcuts (Japan, Edo period) and Rembrandt's etchings are better explained through art historical accounts than through differences in internal brain organization. The possible ways in which a human figure can be drawn are constrained by the human visual system. Our perceptual preference for clear-cut shapes (Cavanagh, 2005) may account for the strong delineated shapes and the absence of shadow in many artistic traditions, for instance in the Japanese Edo period woodcuts that portray human figures. These strong lines also allow for the depiction of implied motion and imbalance in the human figures (e.g., sword-fighting or standing on one leg) in Hokusai's *Manga* (1814). Indeed, a recent fMRI study indicates that motion-sensitive areas of the extrastriate visual cortex are recruited when participants look at these images (Osaka, Matsuyoshi, Ikeda, and Osaka, 2010). By contrast, Rembrandt's use of shadows and diffuse shapes provides more static, almost rigid figures, but allows for a more dynamic expression of emotions on their faces – by making facial expressions diffuse, there is room for the observer's interpretation, heightening emotional response (Vuilleumier, Armony, Driver, and Dolan, 2003). Thus, there seems to be a trade-off between clarity of shape and expression of emotions – both are in tune with human perceptual predispositions, but cannot be realized simultaneously. In order to explain the choices that have led to these divergent artistic styles, one needs to consider the cultural and historical context in which they evolved. In the case of the Edo period woodcuts, limitations inherent to the medium of woodcuts and a preference for clear shapes and striking compositions in Japanese visual art may be contributing factors. In the case of Rembrandt's etchings, an increased emphasis on expressing emotions in Baroque art may provide an explanation. In this way, empirical findings from cognitive neuroscience provide building blocks for testable hypotheses on the cultural evolution of stylistic traditions, a topic that is currently underexplored in evolutionary studies of art.

The evolved preference for savannah-like landscapes might explain some recurring features of garden and park design, such as a relatively sparse implantation of trees and the frequent use of water-sources like ponds or fountains, but it does not exhaust the types of landscapes we find attractive. Japanese rock gardens, which consist of large stones surrounded by white raked sand or gravel, are a case in point. In contrast to many other types of gardens, Japanese rock gardens do not contain water; rather, the sand or gravel symbolizes seas, rivers or lakes. The aesthetic appreciation of landscapes seems to be subject to considerable cultural influence. For instance, the enjoyment of the sea and mountains is a relatively recent phenomenon in western culture – these places were thought of as threatening and hostile until well into the 19th century. As Corbin (1988) notes, it was only in the course of the late 18th century that people started to visit the beach for recreational purposes.

This ineluctability of the humanities may be true for many domains of human culture. Consider jet-lag: Suppose scientists were able to explain all its effects through neural and genetic processes (i.e., they uncovered all the relevant neural structures responsible for generating 24-hour wake and sleep rhythms and identified the genes that encode circadian rhythms in humans and other animals; indeed, most of these have been identified; see, e.g., Antle and Silver, 2005, for an overview). Still, this would not explain jets or the recent phenomenon of people habitually making air voyages that span half the globe – for this, we need to resort to historical accounts of jet propulsion and sociological explanations of the rise of mass tourism and inexpensive charter flights to exotic destinations (which in turn is linked to the colonial history of these places). Similarly, a host of factors influence the appreciation and production of art, including the social status, education and economic background of the observer or artist, and the context in which one is exposed to the artwork. Consider listening to a piece of music in a concert hall to hearing it while waiting on the phone: The exact same piece of music can elicit feelings of emotion and exultation in the concert hall, while provoking boredom and irritation at the phone.

Accepting the validity of higher-level accounts of art does not automatically lead to a rejection of reductionism. Weaker forms of pluralism (the position that the study of human behavior, including art, requires multiple autonomous perspectives) pragmatically imply that a given phenomenon can be studied by a variety of perspectives – there is no objective reason why lower-level or higher-level accounts should be the only ones worth pursuing. Since scholars are also interested in various properties of art that are not part of human biology, they can legitimately study these through the humanities. For instance, prevailing Buddhist and Taoist influences among Chinese scholars adequately explain the emergence of landscape painting in the Southern Song period and its persistence throughout the Ming dynasty (Cheng, 1991). We can therefore maintain that evolved neural circuits in the human brain can account for the production and appreciation of art. But there must be more to the study of art than simply stating that it can be reduced to the physical structure of the brain. A promising line of research is to investigate how evolved aesthetic preferences causally relate to existing styles, formats and themes in artistic production across the world. Such an account could help us gain insight into why some art forms are more salient than others. For example, it seems puzzling that figurative visual art is more prevalent and more appealing to naive observers than abstract art, although the latter taps more directly into very early stages of evolved perceptual preferences. Indeed, to some authors (e.g., Hodgson, 2006), abstract art is most successful in tapping into primary visual areas, because of the prevalence of bold lines and colors. Maybe art observers not only use aesthetic value to gauge artworks, but also other evaluative criteria, such as the perceived difficulty in making the design. For abstract art, the expertise of the maker is often less easy to judge than it is for naturalistic representations. The search for causal mechanisms in the human brain may well be the most powerful strategy to account for cross-cultural universal patterns in artistic production and appreciation, with the potential of unifying sciences dedicated to the study of art.

Acknowledgements: Elements of this paper were presented at the 16th Annual Meeting of the European Society for Psychology and Philosophy, Utrecht University, June 26-28, 2008. We wish to thank Johan Braeckman and Jean Paul van Bendegem for their comments on an earlier version of this paper. The manuscript has greatly benefited from insightful comments by two anonymous reviewers. This research is supported by grant COM07/PWM/00I from Ghent University and the Research Foundation Flanders.

Received 24 August 2010; Revision submitted 14 November 2010; Accepted 16 November 2010

References

Aiken, N. E. (1998). *The biological origins of art.* Westport, CT: Praeger.

Allen, M. L., Bloom, P., and Hodgson, E. (2010). Do young children know what makes a picture useful to other people? *Journal of Cognition and Culture, 10*, 27-37.

Anderson, R. L. (1989). *Art in small-scale societies*. Englewood Cliffs, NJ: Prentice Hall.

Antle, M., and Silver, R. (2005). Orchestrating time: Arrangements of the brain circadian clock. *Trends in Neurosciences, 28*, 145-151.

Austen, J. (1811[1986]). *Sense and sensibility.* London: Penguin.

Barrett, H. C., and Kurzban, R. (2006). Modularity in cognition: Framing the debate. *Psychological Review, 113*, 628-647.

Barry, A. M. (2006). Perceptual aesthetics: Transcendent emotion, neurological image. *Visual Communication Quarterly, 13*, 134-15l.

Bechtel, W., and Mundale, J. (1999). Multiple realizability revisited: Linking cognitive and neural mental states. *Philosophy of Science, 66*, 175-207.

Bekoff, M. (2009). Animal emotions, wild justice and why they matter: Grieving magpies, a pissy baboon, and empathic elephants. *Emotion, Space and Society, 2*, 82-85.

Berlyne, D. E. (1974). *Studies in the new experimental aesthetics. Steps toward an objective psychology of aesthetic appreciation.* Washington, D.C.: Hemisphere.

Blood, A. J., and Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences USA, 98*, 11818-11823.

Brown, D. E. (1991). *Human universals*. New York: McGraw-Hill.

Brown, S., Martinez, M. J., and Parsons, L. M. (2006). The neural basis of human dance. *Cerebral Cortex, 16*, 1157-1167.

Caramazza, A., and Mahon, B. Z. (2003). The organization of conceptual knowledge: The evidence from category-specific deficits. *Trends in Cognitive Sciences, 7*, 354-36l.

Carroll, N. (2004). Art and human nature. *Journal of Aesthetics and Art Criticism, 62*, 95-107.

Casati, R. (2008). The copycat solution to the shadow correspondence problem. *Perception, 37*, 495-503.

Cavanagh, P. (2005). The artist as neuroscientist. *Nature, 434*, 301-307.

Cheng, F. (1991). *Vide et plein. Le langage pictural chinois*. Paris: Editions du Seuil.

Conard, N. J. (2003). Palaeolithic ivory sculptures from southwestern Germany and the origins of figurative art. *Nature, 426*, 830-832.

Corbin, A. (1988). *Le territoire du vide: L'occident et le désir du rivage (1750-1840)*. Paris: Aubier.

Cosmides, L., and Tooby, J. (1994). Origins of domain specificity: The evolution of functional organization. In L. Hirschfeld and S. A. Gelman (Eds.), *Mapping the mind. Domain specificity in cognition and culture* (pp. 85-116). Cambridge: Cambridge University Press.

Costa, M., and Corazza, L. (2006). Aesthetic phenomena as supernormal stimuli: The case of eye, lip, and lower-face size and roundness in artistic portraits, *Perception, 35*, 229-246.

Davies, S. (2005). Ellen Dissanayake's evolutionary aesthetic. *Biology and Philosophy, 20*, 291-304.

Davies, S. (2006). Aesthetic judgement, artworks and functional beauty. *Philosophical Quarterly, 56*, 224-24l.

De Smedt, J. (2009). Cognitive modularity in the light of the language faculty. *Logique et Analyse, 208*, 373-387.

De Smedt, J., and De Cruz, H. (in press). The emergence of art as a universal human behaviour: Adaptation, byproduct, or cultural group selection? In T. Reydon and K. Plaisance (Eds.), *Philosophy of behavioral biology*. Berlin: Springer.

Di Dio, C., Macaluso, E., and Rizzolatti, G. (2007). The golden beauty: Brain response to classical and renaissance sculptures. *PLoS One, 2*, e210l.

Dissanayake, E. (1995). *Homo aestheticus: Where art comes from and why*. Seattle: University of Washington Press.

Dissanayake, E. (2000). *Art and intimacy: How the arts began.* Washington, D.C.: University of Washington Press.

Dunbar, R. I. M., and Barrett, L. (2007). Evolutionary psychology in the round. In R. I. M Dunbar and L. Barrett (Eds.), *Oxford handbook of evolutionary psychology* (pp. 3-

9). Oxford: Oxford University Press.

Dutton, D. (2009). *The art instinct: Beauty, pleasure and human evolution*. Oxford: Oxford University Press.

Farroni, T., Johnson, M. H., Menon, E., Zulian, L., Faraguna, D., and Csibra, G. (2005). Newborns' preference for face-relevant stimuli: Effects of contrast polarity. *Proceedings of the National Academy of Sciences USA, 102*, 17245-17250.

Fastl, H., and Zwicker, E. (2007). *Psychoacoustics. Facts and model*s. Berlin: Springer.

Feruglio, V. (2006). De la faune au bestiaire—La grotte Chauvet—Pont-d'Arc, aux origines de l'art pariétal paléolithique. *Comptes Rendus Palevol, 5*, 213-222.

Fitch, T. E. (2005). The evolution of music in comparative perspective. *Annals of the New York Academy of Science, 1060*, 29-49.

Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L., Miller, P. J. O., and Hoelzel, A. R. (2006). Killer whales are capable of vocal learning. *Biology Letters, 2*, 509-512.

Gallagher, H. L., and Frith, C. (2003). Functional imaging of 'theory of mind.' *Trends in Cognitive Sciences, 7*, 77-83.

Garavan, H. (2010). Insula and drug cravings. *Brain Structure and Function, 214*, 593-601.

Geary, D. C. (1995). Reflections of evolution and culture in children's cognition. Implications for mathematical development and instruction. *American Psychologist, 50*, 24-37.

Geissmann, T. (2000). Gibbon songs and human music from an evolutionary perspective. In N. L. Wallin, B. Merker, and S. Brown (Eds.), *The origins of music* (pp. 103-123). Cambridge, MA: MIT Press.

Gell, A. (1998). *Art and agency. An anthropological theory.* London: Clarendon Press.

Gill, K. Z., and Purves, D. (2009). A biological rationale for musical scales. *PLoS One, 4*, e8144.

Gombrich E. H. (1995). *Shadows: The depiction of cast shadows in western art*. London: National Gallery.

Gottschall, J., and Wilson, D. S. (Eds.). (2005). *The literary animal. Evolution and the nature of narrative.* Evanston, IL: Northwestern University Press.

Greenberg, C. (1991). Avant-garde and kitsch. In S. Everett (Ed.), *Art theory and criticism: An anthology of formalist, avant-garde, contextualist and post-modernist thought* (pp. 26-40). Jefferson, NC: McFarland.

Hauser, M. D., and McDermott, J. (2003). The evolution of the music faculty: A comparative perspective. *Nature Neuroscience, 6*, 663-668.

Hinde, R., and Barden, L. (1985). The evolution of the teddy bear. *Animal Behaviour, 33*, 1371-1373.

Hodgson, D. (2006). Altered states of consciousness and palaeoart: An alternative neurovisual explanation. *Cambridge Archaeological Journal, 16*, 27-37.

Hokusai, K. (1814). *Hokusai manga*. Nagoya: Eirakudo.

Huron, D. (2004). The plural pleasures of music. In J. Sundberg and W. Brunson (Eds.), *Proceedings of the 2004 music and music science conference* (pp. 65-78). Stockholm: Kungliga Musikhögskolan Förlaget.

Kanazawa, S. (2000). Scientific discoveries as cultural displays: A further test of Miller 's courtship model. *Evolution and Human Behavior, 21*, 317-321.

Koops, W. (1996). Historical developmental psychology: The sample case of paintings. *International Journal of Behavioral Development, 19*, 393-413.

Latto, R. (1995). The brain of the beholder. In R. L. Gregory, J. Harris, P. Heard, and D. Rose (Eds.), *The artful eye* (pp. 66-94). Oxford: Oxford University Press.

Levinson, J. (1993). Extending art historically. *Journal of Aesthetics and Art Criticism, 51*, 411-423.

Levitin, D., and Menon, V. (2003). Musical structure is processed in “language” areas of the brain: A possible role for Brodmann Area 47 in temporal coherence. *Neurolmage, 20*, 2142-2152.

Lorenz, K. (1943). Die angeborenen Formen möglicher Erfahrung. *Zeitschrift für Tierpsychologie, 5*, 235-409.

Maess, B., Koelsch, S., Gunter, T., and Friederici, A. (2001). Musical syntax is processed in Broca’s area: An MEG study. *Nature Neuroscience, 4*, 540-545.

Mag Uidhir, C., and Magnus, P. D. (in press). Art concept pluralism. *Metaphilosophy.*

Mahon, B. Z., Anzellotti, S., Schwarzbach, J., Zampini, M., and Caramazza, A. (2009). Category-specific organization in the human brain does not require visual experience. *Neuron, 63*, 397-405.

Martindale, C. (1998). Bouguereau is back. Retrieved on November 15, 2009 from http://www.science-of-aesthetics.org/proceedings/abwed.html.

Martindale, C., and Uemura, A. (1983). Stylistic evolution in European music. *Leonardo, 16*, 225-228.

Mell, J. C., Howard, S. M., and Miller, B. L. (2003). Art and the brain. The influence of frontotemporal dementia on an accomplished artist. *Neurology, 60*, 1707-1710.

Miall, R., Gowen, E., and Tchalenko, J. (2009). Drawing cartoon faces—A functional imaging study of the cognitive neuroscience of drawing. *Cortex, 45*, 394-406.

Miller, B. L., Cummings, J., Mishkin, F., Boone, K., Prince, F., Ponton, M., and Cotman, C. (1998). Emergence of artistic talent in frontotemporal dementia. *Neurology, 51*, 978-982.

Miller, G. (1999). Sexual selection for cultural displays. In R. Dunbar, C. Knight, and C. Power (Eds.), *The evolution of culture. An interdisciplinary view* (pp. 71-91). Edinburgh: Edinburgh University Press.

Miller, G. (2000). *The mating mind. How sexual choice shaped the evolution of human nature.* London: William Heineman.

Morris, P. H., Reddy, V. and Bunting, R. C. (1995). The survival of the cutest: Who’s responsible for the evolution of the teddy bear? *Animal Behaviour, 50*, 1697-1700.

Nettle, D. and Clegg, H. (2006). Schizotypy, creativity and mating success in humans. *Proceedings of the Royal Society B, 273*, 611-615.

New, J., Cosmides, L., and Tooby, J. (2007). Category-specific attention for animals reflects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences USA, 104*, 16598-16603.

Orians, G. H., and Heerwagen, J. H. (1992). Evolved responses to landscapes. In J. Barkow, L. Cosmides, and J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 555-579). New York: Oxford University Press.

Osaka, N., Matsuyoshi, D., Ikeda, T., and Osaka, M. (2010). Implied motion because of instability in Hokusai manga activates the human motion-sensitive extrastriate visual cortex: An fMRI study of the impact of visual art. *NeuroReport, 21*, 264-267.

Osborne, H. (1981). What is a work of art? *British Journal of Aesthetics, 21*, 3-11.

Ostrovsky, Y., Cavanagh, P., and Pawan, S. (2005). Perceiving illumination inconsistencies in scenes. *Perception, 34*, 1301-1314.

Pascalis, O., and Bachevalier, J. (1998). Face recognition in primates: A cross-species study. *Behavioural Processes, 43*, 87-96.

Pinker, S. (1997). *How the mind works.* London: Allen Lane.

Rabinovich, R., Gaudzinski-Windheuser, S., and Goren-Inbar, N. (2008). Systematic butchering of fallow deer (*Dama*) at the early Middle Pleistocene Acheulian site of Gesher Benot Ya'aqov (Israel). *Journal of Human Evolution, 54*, 134-149.

Racette, A., and Peretz, I. (2007). Learning lyrics: To sing or not to sing? *Memory and Cognition, 35*, 242-253.

Ramachandran, V. S., and Hirstein, W. (1999). The science of art. *Journal of Consciousness Studies, 6*, 15-51.

Seeberger, F. (2003). *Klangwelten der Altsteinzeit.* CD recorded for Urgeschichtliches Museum, Blaubeuren, Germany.

Seifert, L. S. (1992). Experimental aesthetics: Implications for aesthetic education of naive art observers. *Journal of Psychology, 126*, 73-78.

Snowdon, C. T., and Teie, D. (2010). Affective responses in tamarins elicited by species-specific music. *Biology Letters, 6*, 30-32.

Solso, R. L. (2000). The cognitive neuroscience of art: A preliminary fMRI observation. *Journal of Consciousness Studies, 7*, 75-85.

St. Cartmail, K. (1997). *The art of Tonga. Ko e ngaahi'aati'o Tonga*. Honolulu: University of Hawai'i Press.

Steel, D. (2004). Can a reductionist be a pluralist? *Biology and Philosophy, 19*, 55-73.

Taylor, M., and Carlson, S. M. (1997). The relation between individual differences in fantasy and Theory of Mind. *Child Development, 68*, 436-455.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20*, 410-433.

Tolstoy, L. (1878[1995]). *Anna Karenina* (translated by Maude, L., and Maude, A.). Ware, Hertfordshire, UK: Wordsworth.

Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O. and Kanwisher, N. (2000). Response properties of the human fusiform face area. *Cognitive Neuropsychology, 17*, 257-280.

Tooby, J., and Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, and J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19-136). New York: Oxford University Press.

Tooby, J., and Cosmides, L. (2001). Does beauty build adapted minds? Toward an evolutionary theory of aesthetics, fiction and the arts. *SubStance, 30*, 6-27.

Van Damme, W. (1997). Do non-western cultures have words for art? An epistemological prolegomenon to the comparative study of philosophies of art. In E. Benitez (Ed.), *Proceedings of the Pacific Rim conference in transcultural aesthetics* (pp. 97-115). Sydney: University of Sydney.

Van de Walle, G., Rubenstein, J., and Spelke, E. S. (1998). Infant sensitivity to shadow motions. *Cognitive Development, 13*, 387-419.

Vartanian, O., and Goel, V. (2004). Neuroanatomical correlates of aesthetic preference for paintings. *NeuroReport, 15*, 893-897.

Vuilleumier, P., Armony, J. L., Driver, J., and Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience, 6*, 624-631.

Wright, A. A., Rivera, J. J., Hulse, S. H., Shyan, M., and Neiworth, J. J. (2000). Music perception and octave generalization in rhesus monkeys. *Journal of Experimental Psychology: General, 129*, 291-307.

Zaidel, D. W. (2005). *Neuropsychology of art. Neurological, cognitive and evolutionary perspectives.* Hove: Psychology Press.

Zeki, S. (1998). Art and the brain. *Daedalus, 127*, 71-103.

Zeki, S. (1999). *Inner vision. An exploration of art and the brain.* New York: Oxford University Press.

Zeki, S., and Marini, L. (1998). Three cortical stages of colour processing in the human brain. *Brain, 121*, 1669-1685.