Art-making evolved mostly to attract mates
By Geoffrey Miller

Published as:
Miller, G. F. (2016). Art-making evolved mostly to attract mates. In On the origins of art [exhibition catalog] pp. 163-213. Hobart, Tasmania: Museum of Old and New Art.

Why did art evolve?

The question seems simple. But it can't be answered cogently without playing by the rules of modern evolutionary theory[1]. If you don't play by those rules, you're free to dream up any origin myth that seems appealing. Many folks have. Typical art-origin myths offer a heady mix of neuro-babble, paleo-sentimentalism, artwank pretentiousness, and naïve group selection[2]. However, if you want the *right* answer, rather than just a cute story, you have to dig deeper.

But why did art evolve, really?

Let's start with a simple point: in biological terms, human art is just another "signaling system", like bee dances, bird songs, or gorilla chest-thumping. It's much more complicated, but the signaling principles are the same. Over the last 40 years, evolutionary biologists, anthropologists, and economists have developed a cool field called signaling theory that describes how signaling systems work, and what counts as a credible explanation for their emergence. It's a good theory, and it's worked really well to illuminate animal communication in thousands of species. If a theorist isn't invoking signaling theory when talking about the evolution of a signaling system, like human art, you know they're trying to spin a rivulet of feculence into a pearl necklace. Don't buy it.

In any signaling system, a set of "signalers" (e.g. artists) evolve the abilities and motivations to create a set of "signals" (e.g. art-works) to influence the behavior of a set of "receivers" (e.g. the art-viewers and artist-admirers).

Here's the thing: it's usually much harder to explain why the signalers bother to send the signals, than to explain the "receiver psychology" of why onlookers bother to pay attention to the signals. Receiver psychology is easy. It starts out as just whatever set of brain-biases exist in your species: the perceptual, cognitive, emotional, social, sexual, and ideological sensitivities that influence your aesthetic tastes and preferences.

An iris painting by Mark Quinn: Receiver psychology. Human eyes served two functions in mate choice: as perceptual systems, they guide visual preferences for faces, bodies, and artefacts, but as objects of sexual selection, the white sclera reveals physical health, the irises diversified in coloration in different populations (possibly through runaway sexual selection), and subtle muscle tensions around the eye reveal emotions, social intelligence, and mental health.

If you argue that "art is just the cheesecake of the mind", then you're focused only on receiver psychology and our sensory biases. Cheesecake tastes good because we evolved tastes for fat and sweet; art looks good because we evolved visual systems for orienting towards objects, people, and landscapes that show strong cues of novelty, distinctiveness, and relevance to fitness[3]. Fair enough – but you haven't explained why signalers make art. You've explained the consumers but not the marketers, the groupies but not the rock stars. Likewise, if you argue that "art arises from the visual system's intrinsic pattern-detection abilities" or some such, you're equally focused on receiver psychology.

Painting (from Opticromías exhibition, 2015) by Felipe Pantone: Cheesecake of the visual cortex? Non-representational art that includes strong contrasts, crisp line segments, depth cues, and saturated colors could be interpreted as mere "eye candy" that plays upon receiver

psychology, stimulating key regions of the visual cortex. However, from Bridget Riley's Op Art onwards, it takes considerable skill to fashion an artefact out of canvas and paint that can achieve these effects. By focusing on the skills required for art-making rather than the mechanisms involved in vision, we can reinterpret an apparently arbitrary collection of strong visual stimuli as an impressive – and attractive – display of creativity and virtuosity.

Le Due Luci (2012) by Roberto Bernardi. This photorealistic painting could be construed as literal eye candy, but that would be overlooking the great skill required to capture these nine treats with brush and pigment – especially the play of light on the cellophane wrappers.

Monkeys as Judges of Art (1889) by Gabriel von Max. The limits of receiver psychology. Another problem with the eye candy theories of art-making is that closely related primates with very similar visual systems just don't respond to artistic images or sculptures the way that humans do – with an eye for the skill, intelligence, and creativity behind the art-making process.

Au revoir Zaire by Walton Ford. A male African grey parrot – one of the world's most intelligent birds – creates an elaborate fruit-baited trap to copulate with a gullible female.
The eye candy theory of art evolution has this problem: any arbitrary aesthetic preference can be exploited to distract, manipulate, and seduce the receiver. Unless the aesthetic response benefits the receiver on average, natural selection would quickly eliminate such vulnerabilities. Females who ignore the eye candy would escape the rape and the noose, and would leave offspring less easily bedazzled. Signaling systems are evolutionarily stable only when they bring net fitness benefits to both signalers and receivers.

Negai no Itoguchi (Unravelling the Threads of Desire), Ukiyo-we woodblock print (18th C) by Kitagawa Utamaro. The sexual selection theory of art-making is about the evolutionary functions of art, not about the content of art. Actually, explicit sexual content is often better explained by the eye candy theory, because it's usually produced for males to fantasize about in private, not to attract mates of either sex. Many artists across cultures have supplemented their income by producing erotica, but are often somewhat embarrassed to produce it – it's the opposite of a status-enhancing public signaling strategy.

Receiver psychology is fun to analyze – what makes something great "eye candy"? You can bring the whole armamentarium of the behavioral sciences to bear on understanding how people's minds and brains respond to various aesthetic stimuli. You could get big neuroscience grants to show people Rubens versus Rothkos in fMRI machines and see which brain areas light up[4]. You could wire museum-goers up to mobile psychophysiology devices to assess galvanic skin responses (sweats, palpitations, panic) when viewing German Expressionism[5]. You could study how people with autism versus paranoid schizophrenia respond to Marina Abramovic videos. You could assess the genetic overlap between preferences for Thomas Kinkade's real kitsch and preferences for Jeff Koons' ironic kitsch in a large sample of Swedish twins.

Manet (1991) by Jeff Koons. Ironic porn kitsch illustrating the reproductive success of male artists. Part of his edgy 'Made in Heaven', this self-portrait shows the artist going down on his newlywed wife, Hungarian-Italian porn star Ilona Staller, aka 'Cicciolina', who was also a libertarian member of the Italian parliament. Their son Ludwig was born within a year. Koons also sired a daughter in art school, and had six further children with his current wife, Justine Wheeler. With a net worth of about $100m, Koons is one of the richest living artists, and one of the most genetically prolific. The work's title references Édouard Manet, and hints at his most controversial work, Le Déjeuner sur l'herbe (The luncheon on the grass), although the setting here, instead of a soft pastoral glade, is hard-core rocks in front of an apparently radioactive green pond. This would increase the mutation load of any resulting offspring, so it is not an ideal place to mate.

The Painter's Honeymoon (1864) by Frederick Leighton. A gentler image about the reproductive success of male artists. A young bride admires her new husband's newest work. I liked this

image enough to use it on the cover of my book "Mating intelligence: Sex, relationships, and the mind's reproductive system".

The Artist's Wife Emma, on her Wedding Day (1853) by Ford Madox Brown. After his first wife's death, Brown (1821-1893) eloped with his model Emma Hill (1829-1890) in 1849, and their first child was born in 1850. Three years later, they wed. Her expression seems sleepily post-coital.

However, none of that receiver psychology matters very much for explaining the signaler side of the equation. The key question in any evolved signaling system is: *why do the signalers bother*? Why do they invest their limited time, energy, and risk in growing ornaments, making sounds, or creating works that receivers might enjoy? Once signalers are giving away gobs of potentially useful information to anyone within visual range, it's not surprising that receivers evolve to pay attention to the new info-flood.

Here's an example. Female bowerbirds have eyes and brains tuned to perceive visual depth using convenient cues; this makes their depth perception systems vulnerable to perspective illusions. You could do perceptual psychology studies on this part of their receiver psychology, if you wanted. But males of one species, the Great Bowerbird (*Ptilonorynchus nuchalis*) have evolved to build their courtship bowers to create an ingenious forced-perspective illusion when females view the bower's court through the central avenue, making the male look bigger when he displays in front of his bower. The quality of each male's forced-perspective illusion predicts his mating success[6], so females are not just fooled by the perspective illusion; they implicitly use the illusion's quality as a cue of the male's mate value. And the males take years to learn how to construct the most effective forced-perspective illusion.

A Great Bowerbird's forced-perspective illusion. On the left, he's arranged stones behind his nest with the largest ones closest to the (female bowerbird) viewer, and smaller ones behind, to increase his apparent size when he displays in front. He doesn't need to consciously understand the female brain's depth-perception system; he just evolved to make his art installation play upon her receiver psychology. On the right, a naughty scientist has rearranged the bird's stones with the smallest in front and the largest in back, negating the depth illusion. The bowerbird will quickly rearrange the stones to restore the illusion and his own mating prospects.

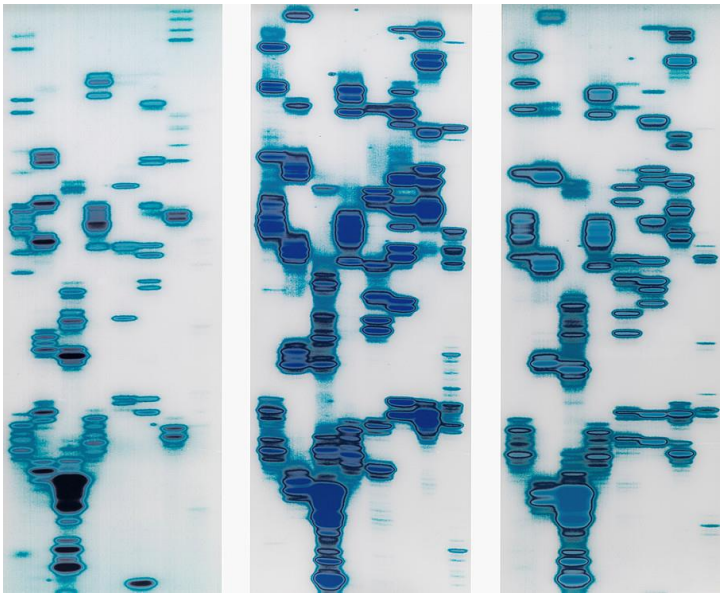
So we should rephrase our central question: not why receivers evolved to respond to art, but why signalers evolved to make art.

How did art-making evolve?

A full century before signaling theory, back in 1871, Charles Darwin proposed a damned good theory of art-making. He didn't get it 100% right, but I think he got it at least 80% right.

Darwin suggested that "art" emerged long before humans. It arose to attract sexual partners, by showing conspicuous beauty, skill, and creativity. From the sexual ornaments of iridescent beetles to the courtship architecture of bowerbirds, animals grow art on their bodies or make art in their environment, to signal their health, resourcefulness, intelligence, and/or general fitness. Aesthetic ornamentation reveals good genes, good bodies, and good brains[7].

Sperm Gauge by James Vaughan. If male art-making reveals genetic quality, then male-made art is basically a gauge of sperm quality. Females choosing among male suitors confront a cabinet of curiosities – behind each man's artefacts are the sperm he offers; behind his sperm are the expected future progeny he could sire.



Glenn, Dario, and Tyrone (1998) by Iñigo Manglano-Ovalle. A C-print of genotypes from three men. DNA variants appear as abstract aesthetic patterns, symbolizing heritable variation in creativity, virtuosity, intelligence, and fitness. Since prehistoric humans lacked the technology to genotype potential mates directly, they had to rely on indirect signals of genetic quality – such as art-making ability.

Examples of evolved aesthetic ornamentation:

A flower painting by Mark Quinn. Plants evolved flowers as sexual ornamentation to attract pollinators. Here Quinn uses hyperrealistic representational flair and large scale to attract and impress the human viewer.

Wing of a Blue Roller (1512) by Albrecht Dürer. A masterpiece of naturalistic observation and watercolor skill. Rollers get their name from the aerial acrobatics they perform during courtship, displaying the maneuverability they need to catch flying insects on the wing, and showing off their colorful wings to potential mates. This same year (1512), Dürer starting working on his Four Books on Human Proportion (Vier Bücher von Menschlicher Proportion), which advocated three aesthetic principles: Nutz (function), Wohlgeffalen (naïve approval), and Mittelmass (the happy medium), emphasizing how the artist can create beautiful images using each.

However, Darwin's colleagues could not stomach the idea that the highest achievements of human visual culture could emerge from mere "mating instincts', because they under-estimated the complexity of prehistoric mating and the aesthetic discernment of prehistoric mates. A combination of Victorian misogyny and cultural pretentiousness kept them from seeing the mate-attraction functions of art. With sexual selection banished from the explanatory repertoire of evolutionary aesthetics, art had to arise either through natural selection for survival, or as a non-adaptive side-effect of other biological or cultural processes. After the rise of Modernist art

and architecture in the early 20th century, aesthetic theorists doubled down on rejecting the concepts of “beauty” or “skill”, so the challenge of explaining the evolution of animal beauty or human art-making talent seemed passé.

The Island (2009) by Walton Ford. The nightmare of natural selection. Darwin realized that all populations can undergo exponential growth, so that whatever abundance an environment offers for a few generations, any population will quickly reach carrying capacity. Here some Tasmanian tigers (Thylacinus cynocephalus) are fighting over the last few lambs on an overcrowded island. Humans in turn hunted these carnivorous marsupials to extinction by 1936. Competition for survival favors practicality rather than beauty, efficiency rather than extravagance, species-typical adaptations rather than conspicuous individual differences, and functional innovation rather than playful creativity – so is rather unlikely to explain human art.

Sexual coercion versus female choice:

Judith Beheading Holofernes (1612) by Artemisia Gentileschi. Women exercising their power of mate choice. The Assyrian general Holofernes wanted sex with the beautiful widow Judith on the night before he planned to destroy her city of Bethulia. She got him drunk and sawed off his head, saving her virtue and her home. Artemisia Gentileschi (1593-1656), the best female Baroque painter, painted this around age 19. She offers an especially gritty, bloody, and dramatic scene compared to earlier sanitized and eroticized versions. Judith and her maid hold down Holofernes with a business-like determination, while he struggles not to bleed out. Every rapist has to sleep some time, and then he's vulnerable to moralistic punishment by his victims and their allies. Prehistoric female alliances helped women maintain their power of mate choice against male sexual coercion, giving sexual selection the elbow room to shape kinder, gentler, more creative traits such as art-making in both sexes.

Salome (c. 1900) by Pierre Bonnaud. A different take on women beheading men. With her erotic dancing, Salome seduced Herod, who promised her anything she wished; she demanded the head of John the Baptist on a plate. Here Salome's male kinsmen have already conquered the hostile forces of nature, symbolized by the tiger pelt rug. This gives her the freedom to favor highly encephalized males. She doesn't care about the rest of his body, and neither does he, apparently. It's the heritable brain-power that she's after. Her fingers seem to measuring the size of his prefrontal cortex, a region strongly implicated in general intelligence and creativity.

Ajax & Cassandra (1886) by Solomon J. Solomon: Sexual coercion circumvents female choice. In Greek myth, Apollo blessed the Trojan princess Cassandra with the power of prophecy in an attempt to seduce her, but she refused his advances, so he cursed her never to be believed. Later, during the fall of Troy, the Locrian Ajax abducted Cassandra from the Temple of Athena and brutally raped her. For desecrating her temple, Athena, with the help of Zeus and Poseidon, destroyed most of the Greek fleet returning home from Troy, including sucking Ajax up in a furious whirlwind, penetrating his chest with bolts of magic fire, and throwing him down to be impaled upon sharp rocks. Ouch. Powerful men can use sexual coercion to circumvent female mate choice – but then females can band together with even more powerful men to seek revenge and deter future rapes. Most Victorian biologists (other than Darwin) wrongly assumed that prehistoric males could sexually coerce females without risk or accountability, such that sexual selection through female choice could not have shaped art, music, or language.

Eros (1886) by Solomon J. Solomon: Honest courtship. Eros, the embodiment of love, courts a fertile but half-reluctant woman. He seduces through a combination of affectionate foreplay,

playful domination, and visual ornamentation – white and cerulean wings unfurled, arms draped in gold.

Pan (1898) by Sydney Long: This classic nymphs-and-fauns pastoral scene symbolizes prehistoric multi-male, multi-female hunter-gatherer clans. Within such groups, sexual selection typically entailed mutual mate choice and mutual courtship by both sexes. However, males had sexual incentives to invest more time and energy in public broadcasting of their aesthetic skills, as with the faun playing music. Naïve group-selectionist accounts would interpret the musical effort as providing a common good to the dancing group, perhaps to promote clan solidarity. By contrast, the sexual selection model would focus on the smitten groupie lying on her front, the way her erotic attention is locked onto the musician, and the impending evening's polyamorous-yet-choosy orgy. The fauns are lusty beast from the waist down, but creative artists from the neck up.

Leda and the Swan (2004) by Fernando Botero. In Greek myth, Zeus disguises himself as a swan and seduces or rapes Leda, the Queen of Sparta, siring Helen of Troy. This became a popular theme in the Italian Renaissance (Leonardo, Michaelangelo, Correggio), since swam/woman copulation was seen as less racey than man/woman copulation. Botero made other, rapier versions, in which Leda's face turns away from the swan's head, or the swan pounces on Leda's shoulders as if about to copulate with the back of her neck. Here, though, the sex seems consensual, with intense swan/human eye contact, and an impending kiss. Leda cups her breasts as if to signal her fertility to the King of the Gods, and her body shows a voluptuous sturdiness well suited to birthing demi-gods.

With the renewed application of evolutionary theory to explain human behavior from the 1970s onwards, there have been dozens of speculations about why art arose during human evolution. Most of those speculations fail the most basic criteria for evolutionary theories: they don't

identify the specific selection pressures that favored art-making or art-judging, or the adaptive functions that art served, or the concrete fitness payoffs for making art (in terms of survival and reproduction). Some of these speculations are heart-warming, and raise the social and moral status of art-makers and art-appreciators, so feel ideologically cozy and comforting. Yet most strike me as just-so story-telling and wishful thinking, because they don't get down to brass tacks. They don't address this core issue: how did new genetic mutations for art-making motivations and abilities actually spread among our ancestors, given the real biological costs of art-making in terms of energy, materials, time, and skill-acquisition?

Untitled by Balint Zsako. Beyond sex, almost everything else is hot air. Traditional representational art focuses on the face and upper torso. Here, only the genitals and breasts are depicted, with the rest of the phenotype a vague hot mist. From the gonads' point of view, the rest of the body is just a means to a reproductive end.

Flesh painting (On desire) (2012) by Marc Quinn. Dutch model Lara Stone, heavily pregnant, reclines against red meat. During human evolution, better big-game hunting abilities helped fuel the increased energetic demands of pregnancy, lactation, and larger brains, allowed women to pump out more babies faster than other great apes can afford to do, and gave humans more leisure time to develop the arts than a vegetarian diet would have allowed. Meat, sex, and art come together.

Amotz Zahavi made some progress in 1978 by framing artistic phenomena in signaling theory terms, with his “handicap principle”. He argued that many aspects of ornamental art and decorative patterning are costly, hard-to-fake signals of the artist’s skill. In particular, many decorative patterns make comparative evaluation by observers easier; for example, dots in circles that make it easier to assess radial symmetry; stripes and bars that make it easier to assess body size and proportions. Zahavi wrote presciently[8]:

> “Human society is competitive, so people might be expected to use decorative patterns to advertise quality. I believe that a particular artistic investment by an artist to decorate a product may be understood as a consequence of his attempts to advertise the quality of his product. It may also be an advertisement of the artist’s own artistic qualities. And the ability we have to understand art may have evolved as a consequence of our striving to assess differences in quality using biologically important signals. The theory of optimal decorative patterns may thus form a biological basis for the ultimate ‘advantage’ of art, the evolutionary function of art.” (p. 184).

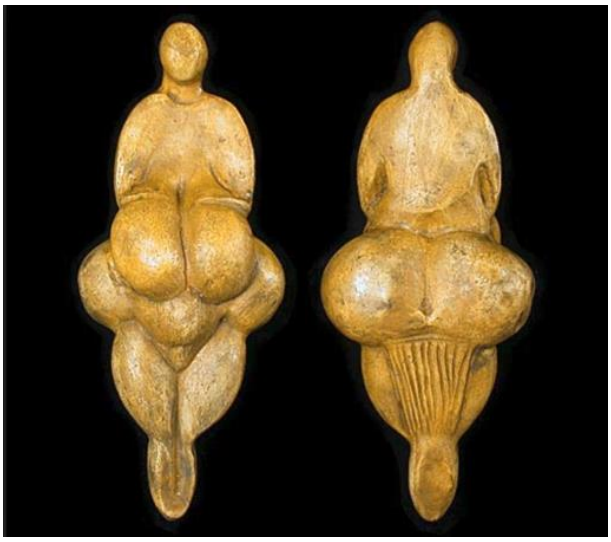
Judgement of Paris I (1982) by Mark Tansey. Female mate choice and the handicap principle. In the original myth, Paris judged between Hera (who offered him power), Athena (who offered wisdom), and Aphrodite (who offered mating with Helen of Sparta, the world’s most beautiful woman). Paris made the aesthetic choice for Aphrodite and Helen, sparking the Trojan war. In Tansey’s Darwinian twist to that myth, female mate choice replaces male mate choice. A woman with a clipboard or notebook chooses among three males trying to signal their fitness. The obstacle course symbolizes Zahavi’s handicap principle: its difficulty is the point. Males who efficiently run around the wall aren’t as impressive as those who scale it.

My Lonesome Cowboy (1998) by Takashi Murakami: Aesthetic signaling is mostly a matter of showing off the quality of one's genes in a conspicuous, stylized, costly way. Here a monumental young manga hero transforms his copious masturbatory ejaculate into an artfully spiraling lasso of love, to intrigue and bind onlooking females.

Fröschenpaar (Frog Pair) (1989) by Renate Rabus. A copulating pair of granular poison frogs (Oophaga granulifera) from Central America. Less than an inch long, their bright coloration evolved mostly as warning coloration to predators that they are poisonous, increasing their survival chances. Warning coloration obeys many of the same costly signaling principles as sexual ornamentation, but tends to occur in both sexes equally, rather than being more conspicuous on males.

Veneration (2007) by Damian Hirst: A butterfly kaleidoscope illustrating signaling on two levels: the sexual selection that shaped the constituent butterflies' bilaterally symmetric ornamentation, and Hirst's radially symmetric arrangement of the butterflies.

Expulsion by Fred Tomaselli. The creative spirit of sexual selection radiates aesthetic ornamentation in every direction – flowers, fruits, beetles, butterflies, body parts, and marijuana buds. Man and woman are overwhelmed by the psychedelic intensity and diversity of life's artistry. They become self-conscious about their own transparently biological bodies and ashamed of their sexuality. They turn away from the Darwinian kaleidoscope. They can't handle the truth. Their self-expulsion from the Garden of Eden is their own choice.



Venus of Lespugne (replica) from Musée de l'Homme. Made about 25,000 years ago in the Pyrenees, about 6 inches tall, carved from tusk ivory. It also illustrates signaling on two levels: the female morphology represented, and the artistic skill to represent it. This Venus is one of the most striking, with highly exaggerated fertility-indicators including large pendulous breasts, a steatopygous butt, fat thighs, and pubic fat, but no facial features or hair. Archaeologists often claim Venus figurines are 'fertility symbols' used in prehistoric magic rites, but a more parsimonious explanation would be Pleistocene porn. The bilateral symmetry is very accurate, suggesting an emphasis on conspicuous precision and fine craftsmanship.

Figure, South Caspian Region, North West Iran, c. 1000 BCE. About 24,000 years after the Venus of Lespugne, here's another stylized female figure, with exaggeratedly low waist-to-hip

ratio indicating high fertility, perky little breasts indicating no previous children, cupped by stick-arms), and simplified facial features.

Since my book *The Mating Mind* in 2000, I've argued that Darwin's hypothesis about art was basically right[9]. Every biologist knows that sexual selection through mate choice favored most of the visual beauty in nature, from the tail-flaps of peacock spiders to the plumage on Birds of Paradise. I just think we can take sexual selection about 20% further, to explain human art-making instincts as well. And we have new scientific insights for doing that. We have deeper insights into animal communication theory to explain how art-making ability can work as a hard-to-fake signal of biological excellence. We have new archaeological evidence on the prehistoric antiquity of beautifully-crafted tools, weapons, body ornamentation, clothing, figurines, and cave paintings. We have new psychological evidence on which heritable traits – physical, mental, emotional, and moral – can be signaled reliably through good art. And we have new models of sexual selection in semi-monogamous species like ours in which both males and females choose their mates and form longer-term pair bonds. We can draw not just from Darwin, but from other evolutionary aesthetic theorists such as Nietzsche, Veblen, Boas, Gombrich, and Zahavi. We can also draw from a century of social progress in which the division between male elite arts and female folk crafts has broken down. Many more women are rediscovered their art-making instincts as parts of their own social and sexual strategies.

A tiny peacock spider (Maratus Volans) displays his tail-flap to attract a female.

Rothschild's Bird of Paradise (1917) by Marian Ellis Rowan. Women rediscovering their art-making instincts. Here a drab female carefully inspects a flamboyant male – all as painted by a talented female natural history artist. In humans, unlike most other species, both sexes create aesthetic ornamentation.

I think this updated expansion of Darwin's art-through-sexual-selection theory is pretty good at explaining why ordinary children enjoy learning how to draw, paint, and dress up (to practice aesthetic courtship skills before puberty), why young single adults enjoy adding visual beauty to their romantic lives in so many ways (to attract partners), and why married adults so often get aesthetically lazy in their dress, decoration, and hobbies (to reduce mating effort as parenting effort takes precedence).

Admittedly, my theory is weaker at explaining the more pretentious and counter-intuitive forms of elite contemporary art. It can't account for why almost 1% of educated urban adults claim to enjoy abstract art, installation art, art-speak, or *Artforum*. But that doesn't matter. Evolutionary psychologists like me seek to explain the 99% -- normal human interest in beauty, artistic skill, visual creativity, and folk arts. I'd rather understand the pop surrealism in *Juxtapoz* than the video installations at Art Basel, because ordinary folks actually *like* and *buy* pop surrealism – and other fun, skilled kinds of representational art. I want to understand the cross-culturally universal forms of artistic passion and skill that provoke spontaneous admiration among ordinary folks. I think the answer is that aesthetic admiration of art shades over into sexual attraction towards the artist – and this has been happening for several thousand generations. We're all descended from artists because art was sexy and art was romantic.

Un Moulage sur Nature (Molding from Nature) (1887) by Edouard Joseph Dantan. Representional painting reveals the methods of representational sculpture. An unusually impressionistic work from a master of technical classicism, depicting an artist and his assistant removing a plaster cast from a model's leg.

Note that art-making is much more ancient than previously believed[10]. It is likely to be long-refined biological adaptation intrinsic to human nature, rather than a recent cultural invention. Until about 2000, archaeologists focused on European cave painting sites and Venus figurines associated with the "Upper Paleolithic revolution" about 30,000 years ago, and claimed little evidence of art-making before that. However, more recent finds push art-making back almost 10x further. By 500,000 years ago, humans were creating Acheulian handaxes with carefully exaggerated symmetry[11], more precise than necessary for killing and butchering animals. By 200,000 years ago, Neanderthals in northern Europe[12] and humans in South Africa[13] were using red ochre, probably for body ornamentation. By 100,000 years ago, humans in South Africa had red-ochre-processing workshops including abalone shell containers, grindstones, and hammerstones to produce body ornamentation pigments on a large scale[14]; similar workshops have been found in the Middle East 92,000 years ago[15]. By 82,000 years ago, humans in North Africa were drilling holes in shells and decorating them with red ochre, presumably for jewelry[16]. Humans have probably been using tattoos, scarifications, and piercings as signals of biological quality for tens of thousands of years[17].

Lower Paleolithic hand axe, Olduvai Gorge, Africa. An unusually large handaxe, 11.4 inches long, 6.5 pounds in weight. It would have been an impractical tool for most purposes, and may represent one of the first examples of art for art's sake, simply showing off the tool-maker's skill.

Acheulian hand axe, c. 500,000 BCE, France. A pretty good hand-axe made from strikingly beautiful stone.

Red ochre has been used for body ornamentation for up to 250,000 years. Here a young woman from the Himba people of Namibia wears red ochre paste on hair and skin.

Red Hill and White Shell (1938) by Georgia O'Keefe: From red ochre to abstract symbolism. A monumental white spiral shell is juxtaposed against an undulating hillscape the color of red ochre. The protruding shell evokes a breast, a clitoris, a skull, an egg, or the visible white sclera of the human eye – but its depth is ambiguous, and it could equally be seen as a spiral receding into the red hillside – a virginal vagina leading back to the uterus and ovaries, or a twisting vas deferens leading back to the epididymides and testicles.

Only much later did art come to serve hundreds of other social, familial, cultural, economic, and ideological functions. Of course those functions are important too – but this exhibition focuses on the evolutionary origins of art, not the cultural applications of art.

How do art-works function as extended phenotypes?

Apart from growing sexual ornaments on their bodies and producing behavioral courtship displays, many animals evolved to create decorations, art-works, constructions, and other physically persistent structures beyond their bodily boundaries, as part of their "extended phenotypes" to attract mates[18]. Extended phenotypes among prehistoric humans had become quite complex by the time of 'Ötzi the Ice-Man', who lived about 5,300 years ago, and whose ice-preserved body was found in the Italian Alps in 1991. When Ötzi died, he was wearing a coat made of alternating light and dark goat hide strips, goat-hide leggings, deerskin shoes, and a leather backpack, and he was carrying a fine copper-bladed axe, a flint-bladed dagger, a yew longbow and fletched arrows, a tree-bast trapping net, and firemaking tinder and flints[19]. Our modern human extended phenotypes reach far beyond our bodies, and include consumer goods and services such as our clothes, cars, houses, art collections, and online dating profiles[20] -- all of which are subject to aesthetic judgment by potential mates.

Oreads (1902) by William Bouguereau. Male mate choice from a sky-river of female fertility. Before Darwin, theorists assumed that physical beauty was the province of the female, with (rich, powerful) males as the chooser. After Darwin, biologists switched to the males display/females choose model of sexual selection. In recent years, a new balance has been struck based on mutual mate choice. From the viewpoint of high-mate-value males like these fauns, sexual selection is what they use to select the most delectable women with the most pleasing physical ornamentation: skin, hair, breasts, buttocks, waists, legs. But from the viewpoint of high-mate-value females, the power of choice remains classically Darwinian – females choosing among males and their aesthetically extended phenotypes.

Other animals have to make rather than buy their extended phenotypes, so their ornamental signals can be very informative about their genetic quality, bodily health, resourcefulness, intelligence, and conscientiousness. This is because it can be physically and cognitively demanding to find and transport the required structural and decorative materials, to choose and defend an optimal display location, to compile the materials skillfully into a form that has the structural integrity to persist in a hostile environment, and to manipulate the art-work to display the aesthetic features to attract mates.

Animal art-works have other advantages as mating signals. In a local mating market, all local materials are equally available to all sexual rivals, so they allow observers to separate variation in environment quality (e.g. how many white shells are available for decorating bowers, how much lapis lazuli is available for making blue paint) from variation in individual genetic quality (e.g. how skillfully a bowerbird can arrange shells or a human painter can grind and apply pigment). Art-works also allow animals to show innovation, creativity, and a tacit understanding of receiver preferences, as when three-spined stickleback fish construct decorative nests of colored algae, and then choose an optimally contrasting color of algae to highlight the nest entrance[21].

Animal art-works can also reliably reveal the animal's bodily size, as when male black wheatear birds carry the heaviest possible stones to ornament their cliffside breeding spots, allowing females to observe their maximum work capacity. These 35-gram birds carry an average of 3 kg of stones per mating (like a 200-pound man carrying 17,000 pounds of stones up a cliff face), and this intense sexual selection on construction ability has resulted in the largest power output of a muscle ever recorded for any species (400 W/kg)[22].

Black wheatear bird carrying material for his art installation to attract a mate.

Many extended-phenotype signals show large size, not just as "supernormal stimuli" exploiting receiver psychology, but using conspicuous waste as a reliable signal of quality and endurance: a 15-cm-tall Vogelkop bowerbird typically constructs a branch-and-twig bower at least 100 cm high and 160 cm in diameter, analogous to a 6' tall human sculptor building a 40'-high, 60'-diameter wooden installation. However, unlike a peacock burdened by a heavy ornamental train, the creator isn't saddled with the burden of carrying around such an enormous sexual ornament: under threat from predators or rivals, the extended phenotype can be abandoned, and the artist can live on to create another day.

A vogelkop bowerbird's large, well-decorated bower attracts mates.

Art-works can be especially efficient signals because they can persist for long periods, out-lasting transient courtship displays (e.g. bird songs or human jokes), and the construction skills they embody can be appreciated and remembered by potential mates even in one's absence. Extended phenotypes are also informative about the creator's vigilance, formidability, and dominance, because they can be sabotaged or stolen by sexual rivals (as when bowerbirds destroy each other's bowers and steal their building materials and ornaments[23]).

The best-studied extended-phenotype signals in other animals that have been shown to attract mates in courtship – and thus the best examples of convergent evolution towards human-style art-making – include:

- silk balloons by at least 100 species of balloon flies (e.g. *Hilara sartor*),
- sand pyramids by ghost crabs (*Ocypode saratan*),
- sand craters by at least 20 species of cichlid fish (e.g. *Cyathopharynx furcifer*),
- flower petal presentations by red-backed fairy wren birds (*Malurus melanocephalus*),
- stone piles at nest cavity entrances by black wheatears (*Onanthe leucura*),
- bowers of twigs and ornaments by 15 species of bowerbirds (e.g. *Amblyornis inornatus*),
- elaborate nests by at least 70 species of weaverbirds (e.g. *Ploceus benghalensis*).

A ghost crab struggles to make a nice sand pyramid to attract mates.

A sand crater made by a cichlid fish to attract mates. Its diameter is more than 10x the fish's body length. Good radial symmetry.

A female weaverbird inspects a male's nest for structural integrity and aesthetic virtuosity.

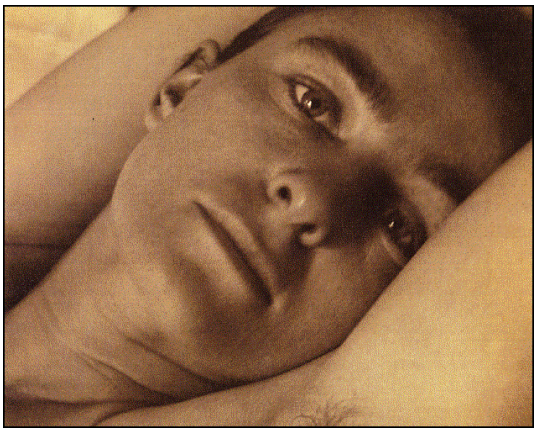
This is a very provisional list, as the study of animal art-works from a signaling theory perspective is still in its infancy, and some of the most skilled creators (e.g. crabs, fish, spiders) are under-studied. And as with many sexually-selected ornaments, the pheromone-obsessed mammals fall short of birds, fish, and invertebrates in the sophistication of their constructions. However, in all cases above, researchers have observed females closely inspecting and comparing male art-works, with direct reproductive payoffs to males who create the best works. So we have examples of sexually-selected extended-phenotype ornamental signals in at least 200 other species that seem functionally analogous to human art-works. That's 200 more examples of convergent evolution than we see for any other theory of human art evolution.

How can we test the sexual selection model for art-making?

The sexual selection model is eminently testable[24]. Indeed, over the last 40 years, biologists have developed some pretty good ways to assess whether a trait evolved as a sexually-selected signal. For example, if human art-making evolved mostly to attract mates, we'd expect it to show most of qualities below. (I note which predictions have supporting evidence so far, and which remain to be tested.)

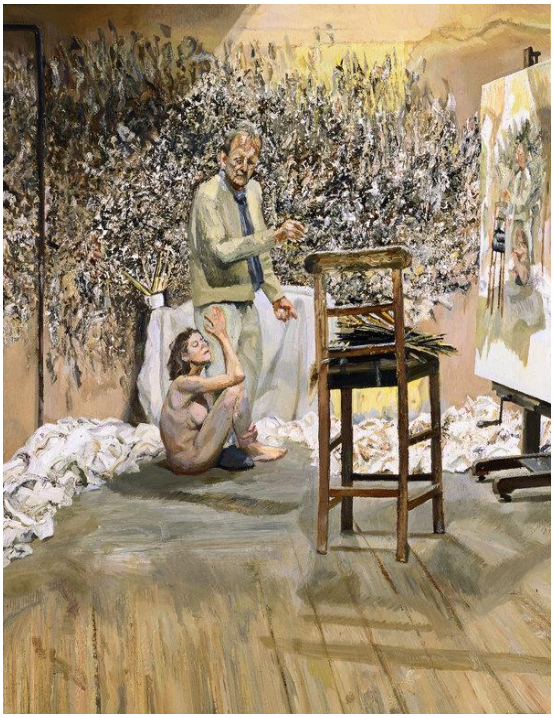
Mate preferences for the trait. All else being equal, art-making should be favored in mate choice by both sexes. In a study of 9,474 people across 37 cultures, males and females ranked

"creative and artistic" as the 7th and 6th most important trait, respectively, out of 13 traits – less important than kindness, intelligence, or health, but more important than earning capacity, education, or religiosity[25]. Women's ovulatory cycles also influence their attraction to artistic creativity and skill: women at the highest fertility phase of the cycle preferred poor but talented visual artists over rich but untalented visual artists[26]. People should be motivated not just to judge artistic skill passively by observing completed works, but to probe actively, witnessing works-in-progress, assessing romantic bespoke works (e.g. a custom portrait of the beloved), and considering works across a variety of forms, materials, and styles. People should feel driven to connect the art-work to the artist, so their extended phenotype illuminates their core phenotype and vice-versa. Art-makers who can talk articulately about their training, skills, intentions, efforts, and aesthetic decisions should be especially attractive, since they reveal high verbal intelligence. As with most behavioral and mental traits, women should be choosier about art-making ability when selecting short-term mates, but men should up-regulate their choosiness about art-making when selecting longer-term mates (e.g. men have low standards for intelligence in one-night stands, but they become as choosy as women when choosing a spouse.) Given mutual mate choice for art-making ability, we also expect positive assortative mating for the trait[27]: couples should correlate for artistic talent and aesthetic sensitivity.



Georgie O'Keefe photographed by her lover Alfred Stieglitz. Assortative mating for art-making ability.

Art-making should attract more mates, especially for male artists. Among 236 visual artists, degree of artistic success strongly predicted mating success for males (e.g. number of male artists' sexual partners correlated +.53 with "time spend on art" and +.45 with "percentage of income from art"); among female artists there was no relationship[28]. In a different study of 708 young adults, males who produced more public creative behaviors (e.g. visual arts, performing arts, writing), attracted more sexual partners, whereas females showed no correlation between creative output and sexual success[29]. Also, more neurotic (worried, anxious) men and more schizotypal (eccentric, disorganized) men displayed more creative activity, which led to more short-term mating success, but the neuroticism and schizotypy boosted sexual success only insofar as it led to creative output; no such patterns appeared for women. Madness leads to mating success only insofar as it's linked to creativity, apparently.



The Painter Surprised by a Naked Admirer (2004) by Lucian Freud. Reproductive success of the male artist. Freud, aged 82 here, paints himself painting himself with a new would-be lover. Freud sired at least 14 children with at least 6 women (2 with his first wife Kitty Epstein, 4 with Suzy Boyt, 4 with Katherine McAdam, 2 with Bernardine Coverley, 1 with Jacquetta Eliot, and 1 with Celia Paul).

Portrait of the Artist's Husband, Charles Beale, in a Black Hat (17th C.) by Mary Beale. Romantic success of the female artist. Mary Beale was the best British female artist of the 17th century, and an advocate of sexual equality and friendship in marriage. After her husband lost his job as

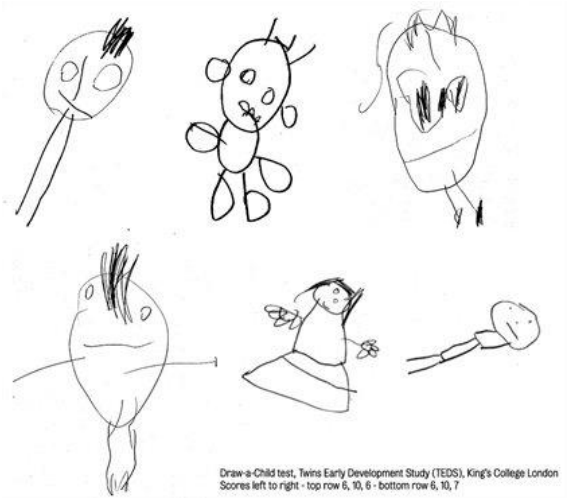
deputy clerk of the patents office, he acted as her adoring business manager. She paints him with startling intimacy and affection.

Genetics of the trait: substantial heritability, elusive molecular-genetic basis, inbreeding depression, and paternal age effects. If art-making abilities function as good genes indicators, they should prove heritable in twin and adoption studies, with artistic ability running in families for genetic and not just environmental reasons. On recent study of 122 twin pairs reared apart showed that the heritability of performance on the "Draw-a-Person" task was at least .38[30]. Also, if genetic variation in art-making ability reflects low mutation load (lower number of harmful mutations that disrupt artistic talent), and these mutations are mostly minor in severity and recent in evolutionary origin, then it should be difficult to find any specific "artistic skill alleles" that replicate across families. Further, art-making should be reduced by genetic inbreeding (e.g. if the artist's parents were first cousins, leading to increased expression of harmful homozygous mutations) and by an individual's dad being older at conception (since sperm mutation load increases with paternal age).

Untitled VI, from 'Bunny series' by Polly Borland. Heritable individual differences. Genes influence the dramatic individual differences that we see in all physical traits – height, body shape, face structure. Here, genetic variation between female bodies embodies different male ancestors' aesthetic ideals that shaped their mate choices; extrapolated into the future, these diverging sexual selection trajectories would result in different subspecies and then species. But genes also influence all psychological traits ever studied, according to twin and adoption studies. Differences in art-making ability are likely to be moderately heritable, so by selecting mates who were good artists, our ancestors could increase the chances that their kids would be good artists in turn.

Genetic correlations with other desirable traits. If art-making abilities function as good genes indicators, they should show genetic overlap ("genetic correlations") with other good traits such as physical health, attractiveness, longevity, fertility, general intelligence, and conscientiousness. One recent study[31] of 7,752 twin pairs found that children's accuracy and detail in drawing human figures at age 4 predicted their IQ scores at age 14, and the genetic

correlation between artistic ability and general intelligence was .52. (Loosely interpreted, this finding suggests that about half of the genetic mutations that make people less intelligent also make them worse at art-making – and vice-versa.) One interesting twist on the genetic correlation argument is that artistic creativity seems genetically linked with some mental illnesses, which might explain their persistence in human populations[32]. In a study of more than 300,000 people with major mental disorders[33], the 54,042 people with schizophrenia were 30% more likely to be visual artists than normal people, and their siblings and offspring were 36% and 38% more likely, respectively, to be visual artists. The 26,644 people with bipolar disorder were 42% more likely to be visual artists, with similar increases among their siblings and offspring. My lab found, though, that it's really general intelligence plus the personality trait of "openness to experience" – and not schizotypy per se – that drives creative drawing ability[34].



Examples from the draw-a-child test by different children aged 4. The more bodily and facial details included at this age, the higher the measured IQ ten years later.

Conspicuous courtship display that tracks mating effort. During courtship, people should conspicuously (if unconsciously) display their art-making abilities and achievements to the opposite sex. For example, when young adults imagine a potential mating situation[35], men score higher on creativity tasks after imagining any potential mate, short-term or long-term. By contrast, women's creativity increases only when they imagine a relationship with a committed, high-quality, long-term mate. People should also make, display, and talk about art more when they're at peak mating age (adolescence and young adulthood) rather than older, when they're single rather than married, and when they're polyamorous rather than monogamous. (Of course, children should be intensely interested in learning and practicing any skill that will be become important in sexual selection after puberty, whether telling stories, making jokes, playing sports, singing songs, or drawing pictures.) Art-making should also be more common when people are in a mating market with a larger number of potential mates, an adverse sex ratio (more within-sex competition), and sexual norms that are more open to short-term mating. At peak fertility, just before ovulation, women's art-making skills should be higher (as most other forms of female physical and behavioral attractiveness peak then[36]), and hormonal contraception such as the Pill should reduce art-making skills at mid-cycle (as it reduces all other forms of peak-fertility attractiveness). Men interacting with ovulating women should show higher mating effort, including more art-making and art-display motivation.

Conspicuous effort: Photo of a very large-scale 'Snow Drawing' by Sonja Hinrichsen. The work is made by walking around in snowshoes for hours in precise patterns.

Production costs that guarantee signal reliability. Sexually attractive, impressive art should be hard to make, and require substantial investment of learning, practice, time, energy, materials, risk, and other resources. Individuals in good condition (good physical health, good mental health, good nutrition, low parasite load) should be able to bear these costs more easily, and this "condition-dependence" of art-making ability should be salient to observers. For example, conspicuous failures of symmetry, precision, or representational accuracy should provoke spontaneous attributions that the artist must have messed up due to bad genes and/or bad condition.

The Löwenmensch (lion-human) from Hohlenstein Stadel cave in Germany, c. 40,000 years ago. Conspicuous precision in one of the oldest works of figurative art. About 12 inches high, it was carved from woolly mammoth ivory using a flint knife, which must have taken many hours. The head is a fine representation of a European cave lion (Panthera spelaea), now extinct.

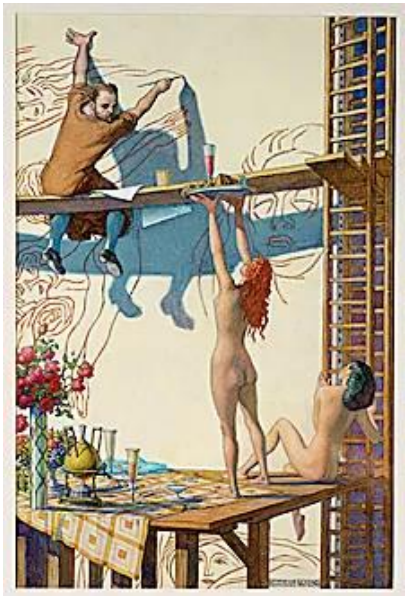
Conspicuous precision in body ornamentation, showing complex knotwork. The great gold belt buckle from the Sutton Hoo ship burial, mound 1 (Anglo-Saxon, early 7th century CE).

Conspicuous precision in decorative art: paper sculpture by Roger Brown. The artist cuts many layers of paper by hand with a scalpel knife. The combination of symmetry and intricacy means that some works take months to complete.

Finis Coronat Opus (1995) by Charles Bell. The game of life rendered with conspicuous precision. The title means 'The end crowns the work', or 'The ends justify the means'. This hyperrealistic painting shows a close-up of pinball machine with a barbarian princess and a halberd-wielding demon, with a ball in play and bonus points accumulating.

Higher trait variance in males. In almost all animal species, the maximum reproductive rate for males is higher than for females – e.g. Gustav Klimt could have potentially sired a new baby every day with a different lover (and he sired at least 14 children with his admirers), whereas a woman who breast-feeds can produce a new baby no more than every couple of years. This higher male reproductive potential favors stronger risk-seeking among males, not just at the behavioral level of violence and extreme sports, but at the level of brain growth and development. The result is higher trait variance in males – e.g. for intelligence, there are more males at the extremes of the bell curve[37]. The same should hold true for art-making ability: we should expect more male artistic geniuses, but also more male artistic idiots who can barely draw, sculpt, or ornament themselves tastefully. The same male risk-taking logic should apply to psychoactive substance use in the service of artistic creativity: Men should seek out and use more drugs to provoke aesthetic inspiration and art-making motivation and diligence[38]. Further, art-making seems associated with having a more masculinized body and brain: a study of 50 artists compared to non-artists found lower 2D:4D digit ratios (ratio of second finger length to fourth finger length) in both males and females. Low 2D:4D is a standard marker of prenatal testosterone exposure[39] that also predicts brain masculinization and increased mating effort.

Portrait of Emilie Louise Flöge (1902), detail, by Gustav Klimt. Flöge (1874-1952) became Klimt's lover when she was 18 and he was 30; she is 28 here. They became lifelong companions, and she became a successful fashion designer in the "rational dress movement". Klimt's most famous work, The Kiss, appears to represent them as lovers. A progressive feminist, she seems to have accepted their open relationship and his many lovers.



Cartoon of Gustav Klimt working on his mural 'Philosophy' (1902) by Remigius Geyling. Klimt's models/groupies offer admiration, wine, food, and sex as he works on one of his most inspiring murals for Vienna University.

Sexual similarities in art-making capabilities. Darwin's hypothesis about art evolution was based on his classic "males compete, females choose" (MCFC) model of sexual selection. That model works well for most species, in which males are not very choosy, and don't invest much in relationships or offspring. However, in species like ours with pair-bonding, social monogamy, committed relationships, and investing fathers, the mutual mate choice (MMC) is more accurate than then MCFC model in making predictions about basic *capacities* for courtship behaviors[40]. So we expect sexual similarity in abilities to make art, even when there are sex differences in

motivations to make art -- just like the sexes are almost exactly equal in average IQ, although men are bigger intellectual show-offs in every domain of intelligence.

Self-portrait (1616) by Artemisia Gentileschi. Painted around age 23 (at peak fertility), Gentileschi signals intelligence, fashion taste, musical talent, and artistic talent. Sexual selection through mutual mate choice predicts sexual equality in art-making abilities, although males are expected to do riskier, higher-cost, more public broad-casting of their artistic talents.

Self Portrait with Nude (1913) by Laura Knight (1877-1970). Knight was the first woman elected to the Royal Academy of Arts, in 1936. She plays around with red ochre tones and depicts the female aesthetic form at three levels: herself in silhouette as the artist, the model from behind as the Male Gaze would objectify her, and her rough painting-in-progress of the model.

Sex differences in display strategies. Higher male potential reproductive rate and risk-seeking should translate into males doing more public broad-casting of their art-making skills, through creating more of the “public” art that ends up in museums and art history records.

Indeed, until the mid-20th century, men produced about 10x more public art than women[41]. By contrast, women should more often narrow-cast their art-making skills towards favored males, to minimize sexual harassment and coercion attempts by undesired males, and to reduce the risk of adverse social judgment by peers. The result is the historical dimorphism between male "high art" and female "domestic arts and crafts". With contraception, increased sexual safety for female public artists, and reduced stigmatization of courtship effort by women, the last several decades have seen an extraordinary increase in women's public art-making. This emerging golden age of female artistic creativity may be due as much to "biological" effects such as these shifts in the social ecology of human mating, as to "cultural" effects such as feminism, economic empowerment, and the rise of art schools and MFAs.

Untitled (1975) by Francesca Woodman. In this self-portrait at age 17, this precocious and influential photographer looks up from a mirror. Her work blossomed shortly after puberty, and reached an unusually high level of innovation by her late teens. However, disappointed by the critical reception to her work, Woodman killed herself at age 22, in 1981. Humans care so much about social reputation that art-making carries existential risks.

Conclusion

Darwin thought that sexual selection offered a pretty good way of explaining the origins and development of our art-making instincts. I agree – especially when we combine sexual selection theory with modern signaling theory, extended phenotype theory, and mutual mate choice theory. The resulting 'mate choice for art-making' theory highlights the functional similarities between human art and aesthetic ornamentation in many other species such as balloon flies, cichlid fish, and bowerbirds. It's also consistent with 9 emerging lines of evidence from the last 25 years of evolutionary psychology and Darwinian aesthetics:

1) People prefer mates who show artistic virtuosity and creativity
2) Skillful art-making attracts more mates, especially for male artists
3) Art-making abilities are moderately heritable
4) Art-making abilities are genetically correlated with other desirable traits
5) Art-making motivation tracks mating effort across ages and relationship status
6) High-quality art requires high costs in resources, energy, time, and skill, so reveals good genes, good condition, and good partner and good parent potential

7) Males show higher variance in the trait (more male artistic geniuses, but also more male artistic idiots, with no skills or taste), reflecting sex differences in reproductive risk-seeking
8) Males and females show equal art-making abilities, due to mutual mate choice
9) Males on average invest more in broadcasting their art-making abilities to multiple potential mates (through larger-scale public art and architecture), while females tend to narrow-cast to potential high-quality mates (through smaller-scale art, craft, and design).

Of course sexual selection doesn't explain everything about contemporary art, for two main reasons.

First, any biological capacity such as art-making that evolved to serve any 'proper' function (the reason why it evolved in the first place) can be exapted, modified, and repurposed to serve many other 'derived' functions, such as signaling tribal affiliation, glorifying religion, designing propaganda for military-industrial states, fetishizing luxury brands, optimizing web sites, marking gang territories with graffiti, or shocking *Artforum* critics at Art Basel. For any theory about art's origins, the number of derived functions will vastly out-number the number of proper functions, because people are creative at adapting our evolved mental traits to new purposes and circumstances.

Second, ever since early-20th-century Modernism, the Western art world has rejected any emphasis on representational skill, pleasant content, or seductive functions as reactionary, bourgeois, or sexist. Most art schools teach MFA students how to talk pretentiously about their 'process' and their 'practice', rather than actually teaching technical processes or requiring any practice. The gallery system creates commercial incentives for every aspiring professional artist to create a unique stylistic brand, rather than building upon a virtuosic tradition. Art critics expound their conceptual responses to works and the artist's alleged intentions and influences, rather than doing investigative journalism about the materials and skills that an artist actually used to produce their works, or their social/sexual/status reasons for doing so. However, that stale old Euro-American Modernist art system faces an existential threat from Asia. Asian art schools have trained a vast new generation of young artists who are equally comfortable with technical virtuosity and conceptual innovation. Art investors are starting to notice that they can buy works that satisfy both their ancient aesthetic instincts for costly trait-signaling, and their post-modernist tastes for stylistic creativity. Skill is making a come-back. The old biophobic cults of Futurism, Abstraction, International Modernism, and Conceptualism are giving way to new biophilic, content-rich movements on the border between art and craft, such as Street Art, Pop Surrealism, and Manga. This, I think, represents a return to Pleistocene art-making instincts and values. Against the dead hand of Modernist art criticism, mass affluence empowers the emerging global middle class to assert their desire to see art that combines virtuosity, creativity, and good old-fashioned sexual charisma.

City Glow (2005) by Chiho Aoshima, one of Japan's leading contemporary female artists. Technical skill combined with conceptual innovation and biophilia, opening a path for future art that satisfies our prehistoric aesthetic instincts more than Modernism ever did. IMHO.

---

[1] Miller, G. F. (2001). Aesthetic fitness: How sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria. *Bulletin of Psychology and the Arts, 2*, 20-25.

[2] Driscoll, C. (2006). The bowerbirds and the bees: Miller on art, altruism, and sexual selection. *Philosophical Psychology, 19*, 507-526.

[3] Miller, G. F. (2007). Reconciling evolutionary psychology and ecological psychology: How to perceive fitness affordances. *Acta Psychologica Sinica, 39*, 546-555.

[4] Brown, S., Gao, X., Tisdelle, L., et al. (2011). Naturalizing aesthetics: Brain areas for aesthetic appraisal across sensory modalities. *NeuroImage, 58*, 250-258.

[5] Tschacher, W., Greenwood, S., Kirchberg, V., et al. (2012). Physiological correlates of aesthetic perception of artworks in a museum. *Psychology of Aesthetics, Creativity, and the Arts, 6*, 96-103

[6] Endler, J. A., Gaburro, J., & Kelley, L. A. (2014). Visual effects in great bowerbird sexual displays and their implications for signal design. *Proc. Royal Society B: Biological Sciences, 281*, e20140235.

[7] Zaidel, D. W., Nadal, M., Flexas, A., et al. (2013). An evolutionary approach to art and aesthetic experience. *Psychology of Aesthetics, Creativity, and the Arts, 7*, 100-109.

[8] Zahavi, A. (1978). Decorative patterns and the evolution of art. *New Scientist, 80*, 182-184.

[9] Miller, G. F. (2000). *The mating mind: How sexual choice shaped the evolution of human nature.* NY: Doubleday.

[10] Morriss-Kay, G. M. (2010). The evolution of human artistic creativity. *J. of Anatomy, 216*, 158-176.

[11] Hodgson, D. (2011). The first appearance of symmetry in the human lineage: Where perception meets art. *Symmetry, 3*, 37-53.

[12] Roebroeks, W., Sier, M. J., Nielsen, T. K., et al. (2012). Use of red ochre by early Neanderthals. *Proceedings of the National Academy of Sciences, 109*, 1889-1894.

[13] Marean, C. W., Bar-Matthews, M., Bernatchez, J., et al. (2007). Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature, 449*, 905-908.

[14] Henshilwood, C. S., d'Errico, F., van Niekerk, K. L., et al. (2011). A 100,000-year-old ochre-processing workshop at Blombos Cave, South Africa. *Science, 334*, 219-222.

[15] Bar-Yosef Mayer, D. E., Vanermeersch, B., & Bar-Yosef, O. (2009). Shells and ochre in Middle Paleolithic Qafzeh Cave, Israel: Indications for modern behavior. *J. of Human Evolution, 56*, 307-314.

[16] Bouzouggar, A., Barton, N., Vanhaeren, M., et al. (2007). 82,000-year-old shell beads from North Africa and implications for the origins of modern human behavior. *Proceedings of the National Academy of Sciences, 104,* 9964-9969.

[17] Koziel, S., Kretschmer, W., & Pawlowski, B. (2010). Tattoo and piercing as signals of biological quality. *Evolution and Human Behavior, 31*, 187-192.

[18] Schaedelin, F. C., & Taborsky, M. (2009). Extended phenotypes as signals. *Biological Reviews, 84*, 293-313.

[19] Miller, G. F. (2014). Stuff: The bare necessities, then and now. *New Scientist*, March 29 (issue 2962), pp. 41-42.

[20] Miller, G. F. (2009). *Spent: Sex, evolution, and consumer behaviour*. NY: Viking.

[21] Ostlund-Nilsson, S., & Holmlund, M. (2003). The artistic three-spined stickleback (*Gastrerosteous aculeatus*). *Behavioral Ecology and Sociobiology, 53*, 214-220.

[22] Soler, M., Martin-Vivaldi, M., Marin, J. M., et al. (1999). Weight lifting and health status in the black wheatear. *Behavioral Ecology, 10*, 281-286.

[23] Wojcieszek, J. M., Nicholls, J. A., & Goldizen, A. W. (2007). Stealing behavior and the maintenance of a visual display in the satin bowerbird. *Behavioral Ecology, 18*, 689-695.

[24] Miller, G. F. (2007). Mating intelligence: Frequently asked questions. In G. Geher & Miller, G. F. (Eds.), *Mating intelligence: Sex, relationships, and the mind's reproductive system* (pp. 367-393). Mahwah, NJ: Erlbaum.

[25] Buss, D. M., Abbott, M., Angleitner, A., et al. (1990). International preferences in selecting mates: A study of 37 cultures. J*. of Cross-Cultural Psychology, 21*, 5-47.

[26] Haselton, M., & Miller, G. F. (2006). Women's fertility across the cycle increases the short-term attractiveness of creative intelligence. *Human Nature, 17*, 50-73.

[27] Hooper, P., & Miller, G. F. (2008). Mutual mate choice can drive ornament evolution even under perfect monogamy. *Adaptive Behavior, 16*, 53-70.

[28] Clegg, H., Nettle, D., & Miell, D. (2011). Status and mating success amongst visual artists. *Frontiers in Psychology, 2*, e310.

[29] Beaussart, M. L., Kaufman, S. B., & Kaufman, J. C. (2012). Creative activity, personality, mental illness, and short-term mating success. *J. of Creative Behavior, 46*, 151-167.

[30] Velazquez, J. A., Segal, N. L., & Horwitz, B. N. (2015). Genetic and environmental influences on applied creativity: A reared-apart twin study. *Personality and Individual Differences, 75*, 141-146.

[31] Arden, R., Trzaskowski, M., Garfield, V., et al. (2014). Genes influence young children's human figure drawings and their association with intelligence a decade later. *Psychological Science, 25*, 1843-1850.

[32] Shaner, A., Miller, G. F., & Mintz, J. (2004). Schizophrenia as one extreme of a sexually selected fitness indicator. *Schizophrenia Research, 70*, 101-109.

[33] Kyaga, S., Lichtenstein, P., Boman, M., Hultman, C., & Långström, N. (2011). Creativity and mental disorder: Family study of 300,000 people with severe mental disorder. *British J. of Psychiatry, 199*, 373-379.

[34] Miller, G. F., & Tal, I. (2007). Schizotypy versus intelligence and openness as predictors of creativity. *Schizophrenia Research, 93*, 317-324.

[35] Griskevicius, V., Cialdini, R. B., & Kenrick, D. T.(2006). Peacocks, picasso, and parental investment: The effects of romantic motives on creativity. *J. of Personality and Social Psychology*, *91*, 63–76.

[36] Miller, G. F., Tybur, J., & Jordan, B. (2007). Ovulatory cycle effects on tip earnings by lap-dancers: Economic evidence for human estrus? *Evolution and Human Behavior*, *28*, 375-381.

[37] Johnson, W., Carothers, A., & Deary, I. J. (2008). Sex differences in variability in general intelligence: A new look at the old question. *Perspectives on Psychological Science, 3*, 518-531.

[38] Miller, G. F. (2011). Optimal drug use and rational drug policy. *Behavioral and Brain Sciences, 34*, 318-319.

[39] Crocchiola, D. (2014). Art as an indicator of male fitness: Does prenatal testosterone influence artistic ability? *Evolutionary Psychology, 12*, 521-533.

[40] Miller, G. F. (2013). Mutual mate choice models as the Red Pill in evolutionary psychology: Long delayed, much needed, ideologically challenging, and hard to swallow. *Psychological Inquiry*, 24, 207-210.

[41] Miller, G. F. (1999). Sexual selection for cultural displays. In R. Dunbar et al. (Eds.), *The evolution of culture* (pp. 71-91). Edinburgh U. Press.