EVOLUTIONARY AND NEURAL NETWORK MECHANISMS OF VISUAL ART ENGAGEMENT

by

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Abstract

Engagement with the visual arts is a universal part of the human experience. By exploring the evolutionary advantages for artistic processes as well as the neural network interactions involved, this review illuminates why humans engage with the visual arts and how our brains allow us to do so. Coming up with creative ideas, tangibly executing them, and aesthetically evaluating artwork all require diverse modes of neurocognitive processing that interact in dynamic ways. As the modern human brain evolved and being able to make and evaluate visual artwork became advantageous to group cohesion and sexual selection, the development of large-scale neural networks facilitated artistic processes. Interactions between functionally diverse networks allows for integration of visual input, executive focus, association formation, salience discernment, emotional valence processing, and reward perception required for artistic processes. The central executive network computes behavior for the attainment of complex cognitive goals that require externally directed attention and inhibition of irrelevant stimuli. The default mode network is conversely activated by internally directed attention on self-referential, social, and intuitive information, spontaneously creating associations that guide artistic conceptualization and insight. While these two networks are functionally oppositional, both executive and spontaneous styles of processing are used within visual art processes; the salience network dynamically regulates activation of the central executive and default mode networks. The salience network additionally processes visual saliency and emotional valence and is interconnected with the dopaminergic reward system, which processes the hedonic value of engaging with art. Unique interactions between these brain networks facilitate visual art engagement, which is ingrained within human cultures for its valuable ability to promote social connection.

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Table of Contents

List of Abbreviations

ACC: anterior cingulate cortex

ATC: anterior temporal cortex

ADHD: attention deficit hyperactivity disorder

AI: anterior insula

ASD: autism spectrum disorder

CEN: central executive network

DA: dopamine

DMN: default mode network

DRS: dopaminergic reward system

fMRI: functional magnetic resonance imaging

fNIRS: functional near-infrared spectroscopy

FTD: frontotemporal dementia

ITC: inferior temporal cortex

MTC: medial temporal cortex

PCC: posterior cingulate cortex

PFC: prefrontal cortex

PPC: posterior parietal cortex

PTSD: post-traumatic stress disorder

SMA: supplementary motor area

SN: salience network

TPJ: temporoparietal junction

Introduction

An important characteristic of the human species is that we are continually and consciously drawn toward the arts (Ramachandran & Hirstein, 1999; Morriss-Kay, 2010). There is evidence for the production of artwork throughout the evolution of modern *Homo sapiens,* with virtually every human culture prioritizing the practice of distinct forms of artistry to this day. The universal human draw toward the arts surpasses cultural, religious, and economic differences (Piechowski-Jozwiak et al., 2017). Though initially attributed to supernatural and religious intervention in early human history, artistic creativity and expression has since become a prevalent area of neurobiological and psychological research (Pavitra et al., 2007). From this scientific focus, we understand that creative insight, art production, and aesthetic evaluation are all functions of the brain. None of these processes are simple or linear forms of computation, activating various regions throughout the brain with different specializations (e.g., Lacey et al., 2011; Chakravarty, 2012; Ellamil et al., 2012; Cela-Conde et al., 2013; Beaty et al., 2015; Kaimal et al., 2017; Vessel et al., 2019). Additionally, understanding why humans evolved to gravitate towards art in such a universally saturated manner requires exploration of multi-faceted theories concerning group survival, language, sexual selection, and the search for quality and novelty within our environments. The purpose of this review is to investigate the evolutionary and neural mechanisms by which the arts have become ingrained within the human species. Artwork is conceptualized, produced, and evaluated by interactions between several large-scale networks within the brain specialized towards differing functions. The central executive network facilitates complex cognitive tasks and goal achievement by holding focus on relevant stimuli (Miller & Cohen, 2001; Chakravarty, 2012); the default mode network allows for imaginative simulations and creative concepts to spontaneously occur (Buckner et al., 2008); the salience network directs our attention towards salient and aesthetically valuable stimuli and is interconnected with the dopaminergic reward system, which promotes the hedonic value of creativity as well as producing and viewing artwork (Takeuchi et al., 2010; Kaimal et al., 2017; Seeley, 2019). A review of literature investigating the involvement of these networks in artistic processes both independently and as a coalition will be discussed, with an emphasis on their evolutionary function, neural mechanisms, and involvement in artistry within humans. This will provide an understanding for the fundamental questions of why humans engage with the visual arts and how our brains allow us to do. In order to understand the evolutionary and neural bases of creative idea generation, art production, and aesthetic evaluation, these terms must first be defined and explored.

Defining art, creativity, and aesthetic experience

The definition of "art" is somewhat ambiguous, as art can be used to describe a perceptible product (i.e., a painting), a process (the flow state an artist enters while in the midst of creation), and/or a concept (the abstract meaning or inspiration expressed or perceived by the viewer). In this review, the use of the word "art" encompasses all three of these aspects: product, process, and conceptualization or idea generation. Specifically, in the following sections an emphasis on the evolutionary and neural bases of art production, creative idea generation, and aesthetic evaluation will be examined. Because this review will not limit art to only one stage of creation, art can be generally defined as a consciously organized expression that gives form to feeling (e.g., Dale et al., 2007). There are countless types of mediums and performance types that can be used as forms of artistic expression.

Inconsistencies across studies examining the neural activity while artists use varying mediums suggest that distinct art forms recruit varying brain structures and networks within the brain (Gonen-Yaacovi et al., 2013). Musical improvisation, dance, and storytelling, for example, are all correlated with different brain structures than drawing or painting. The focus in this review will be on visual artwork, which includes painting, drawing, sculpting, photography, et cetera. As humans have been making visual artwork for up to 40,000 years (Zaidel, 2010; Consoli, 2014), focusing on this form of artistic expression allows for the evolution of neural structures recruited during art production and evaluation to be considered.

Producing original and aesthetically moving pieces of visual art requires the formation of ideas that are usually unconventional, original, and adaptive. These are markers of creativity, which can be defined as the ability to form ideas that are both novel and useful to solve one's current problem or contextualize their environment (Sternberg & Lubart, 1999; Flaherty, 2018). Creativity can also be thought of as cognitive flexibility, which is the ability to adapt thought and behavior towards changing environmental circumstances (Chen et al., 2014). While making effective artwork is generally thought to require creativity, there are cases of significant inborn artistic talent in which little creative thinking is observed. Some autistic artists, despite showing prolific visuospatial talent, create artwork that lacks abstraction, creativity, and originality in comparison to non-autistic artists (Chatterjee, 2011; Pring et al., 2012; Zaidel, 2016). In the case of highly realistic styles of visual artwork, creativity can be viewed as an asset rather than necessity, as novelty is not necessarily a component of figurative work. Visual artwork that is abstract is often also novel and emotionally moving, requiring the ability to think creatively or flexibly (Kandel, 2016). However, figurative artwork does not necessarily lack creativity, as context is important in determining its novelty and usefulness. For example, drawings of neurons made by neuroscientist Santiago Ramón y Cajal were novel and useful at the time in which they were created, both scientifically and artistically (Poole, 2022). Thus, creativity is a function of environmental context as well as artistic content.

Creativity is a multifaceted process (de Souza et al., 2014). One of the first models of creativity designed by Graham Wallas in 1926 identifies four phases in the creative process: preparation (defining the problem), incubation (spending a period of time on the reconstruction of new associations), illumination (creative insight or idea generation), and verification (evaluating the idea for efficacy in solving the problem) (Wallas, 1926). Although numerous models for the creative process have since been published, most share these four common components of preparation, incubation, illumination, and verification (Wiggins et al., 2015). These steps do not necessarily occur in a conscious, linear fashion, however, as there is evidence for alternation between phases as well as the unconscious generation of inspiration (Ellamil et al., 2012). The preparation stage of creativity requires that an individual possess the basic knowledge and skills necessary to develop novel, useful ideas. Thus, basic intelligence is needed in order to acquire, manipulate, and apply information stored throughout the brain. While originality scores on creativity tests have been correlated with an average to above-average IQ, there is not necessarily an intelligence threshold for creative achievement (Jauk et al., 2013). According to Ward et al. (1999), creative capacity as a whole can be considered as an inherent cognitive framework in humans, rather than a selective talent. Individual differences in creativity can thus be attributed to variance in position on personality trait spectrums. Creative people have been found to be more open to experience, impulsive, and unconventional and less conscientious than noncreative people (Feist, 1998). As these traits are heritable (Piffer, 2018), creative potential may be inborn, though creative performance is likely shaped environmentally. Adolescence appears to be a critical period during which people are most susceptible to developing creativity, likely due to the enhanced neuroplasticity during this stage of development (Stevenson et al., 2014). Regardless of age, development in skill requires deliberate practice within a creative domain such as drawing or idea evaluation (Viskontas, 2018). Strengthening creative performance is a function of mindset, with the commitment of time and effort to practice overpowering the inborn degree of creative potential (Piffer, 2018). A meta-analytic study by de Jesus et al. (2013) investigating the relationship between intrinsic motivation and creativity suggests that highly creative people are defined more by their drive and commitment to practice than by their innate talent or intelligence.

Divergent thinking tests are commonly used to measure creative performance, as this thinking strategy is a significant marker of creativity (Mölle et al., 1999; Heilman, 2016; Marron et al., 2018). Divergent thinking can be defined as the ability to create original, variable solutions to open-ended problems (de Manzano et al., 2010). While a single, direct answer is computed in convergent thinking, divergent thinking requires coming up with multiple novel and unusual solutions to a problem (Mölle et al., 1999; Shamay-Tsoory et al., 2011). Randomly produced answers that cannot realistically solve the problem do not follow under the category of divergent thinking, however. This indicates that divergent thinking requires a balance between an open-minded approach to filtering possible answers and the ability to focus on solving the problem at hand. If producing a work of art with a particular emotional expression is the problem, then solving it requires both analysis of conventional solutions (ex- using blue to convey sadness) and the exploration of unexpected ideas (exaltering the surface texture or contour proportion to elicit the desired emotional response). Divergent thinking can be measured using tests such as Guilford's alternate uses test, in which participants must come up with as many alternative uses as possible in a given amount of time for common objects such as a brick, hammer, or comb (de Manzano et al., 2010; Hass & Beaty, 2018). The remote association test measures person's ability to find a common association between unrelated words (Mednick, 1962). Thinking creatively activates the retrieval and combination of remotely associated semantic representations (Mihov et al., 2010); often, the more unconventional the association, the more creative the idea (Mednick, 1962). For any of these tests, answers are generally scored for their originality (coming up with associations not commonly repeated within the sample), fluency (having multiple answers), flexibility (using multiple categories within memory), switching (shifting from one category to another), and elaborateness (having complicated reasoning behind each association) (de Manzano et al., 2010).

Another key aspect of visual art is aesthetic experience. According to Vessel et al., an aesthetic experience is "a perceptual experience that is evaluative, affectively absorbing, and engages comprehension processes" (2019, p. 19155). Visual artwork serves as a major stimulator for aesthetic experience and relies on said experience in order to be effectively expressive. Art, after all, is "a dialogue between artist and viewer" (Morriss-Kay, 2010 p. 160). Visual artwork is arguably produced in order to elicit some sort of emotional or social reactions from others; rarely is artwork created that is not displayed to others (Zaidel, 2010). The value of a painting or other work of art is determined by the viewer, though aesthetic judgement is heavily influenced by the context in which art is being viewed (e.g., Dissanayake, 2000; Wiggins et al., 2015; Kandel, 2012). Kandel (2012) proposes three dimensions of aesthetic evaluation, all of which are driven by memory. First is the initial sensation and recognition of intrinsic elements such as color, form, subject matter, and emotion being depicted. From this basic interpretation develops iconographic evaluation of the meaning of forms, shaped by universal frames of reference. Finally, the viewer builds an iconological interpretation that accounts for one's location, class, religion, culture, historical period, et cetera (Kandel, 2012). Aesthetics thus integrate idiosyncratic memory with raw sensation. Though aesthetic judgements are shaped by individual sensitivity to artistic taste, which is acquired via trained exposure to the arts, key aesthetic features are ranked similarly across experts and non-experts (Hekkert & Van Wiergingen, 1996), demonstrating the universal capability to be emotionally moved by aesthetically pleasing visual artwork. Key features in aesthetically pleasing work are the following: sensory and cognitive accessibility, novelty, tangible relevance, insightful meaning, cultural resonance, and feelings of accomplishment or satisfaction (Dissanayake, 2000). While aesthetic experience is an integral part of art, it is not limited to evaluation of paintings or sculptures. Like creativity, aesthetic evaluation applies to a broad range of environments, objects, and people (Pearce et al., 2016), helping us to differentiate between cues of approach and avoidance.

While humans are not the only organisms capable of thinking creatively or even producing paintings and drawings (Seghers et al., 2014), a tenet of this review is that humans are the only organisms capable of consciously and desirously making visual artwork. Though chimpanzees are capable of dipping brushes into paint and marking a canvas with them (e.g., Martinet & Pelé, 2021), only humans are known to continually make emotionally expressive artwork across cultures separated by time and space. Chimps may enjoy applying color to a surface after being encouraged to do so in captivity, but they do not display painting-like behavior in the wild (Morriss-Kay, 2010). In contrast, humans have continually developed unique artistic practices throughout history. The point at which painting with a brush transitions into being art is dependent on said expression being a conscious, deliberate process intended to elicit an emotional response. Thus, for the purposes of this review, visual art production is a uniquely human phenomenon. This selective focus allows for exploration of *why* we are so drawn to the visual arts, before explaining *how* neural activation allows us to produce and process artwork in such a ubiquitous and complex manner. Humans have the cranial capacity necessary to facilitate the advanced visuospatial, integrative, and imaginative skills used to create works of art (e.g., Miller & Cohen, 2001; Kozbelt & Seeley, 2007; Ellamil et al., 2012; Donahue et al., 2018). However, this does not explain why art is such an integral part of culture. To understand how the visual arts became an ingrained and uniquely human practice, we must explore the evolutionary history of artistic insight, creation, and evaluation.

Evolution of visual art within human cultures

Archeological findings of prehistoric cave art date the emergence of consistent visual art production as 40,000-30,000 years ago during the Upper Paleolithic era, though the oldest known cave markings made by a hominin have been dated back to at least 169,000 years ago (Consoli, 2014; Zaidel, 2016; Hoffmann et al., 2018; Zhang et al., 2021). Multiple hominin species partook in visual art production, with evidence of Neanderthals, *Homo erectus*, and *Homo sapiens* peoples participating in various forms of shell carving, figurine sculpting, body ornamentation and/or cave painting across regions of Africa, Europe, Asia, and Australia (Morriss-Kay, 2010; Joordens et al., 2015; Hoffman et al., 2018). Some such markings cannot necessarily be classified as “artwork”, as they are extremely rudimentary and likely created with little intention. As *Homo sapiens* became the dominant human species, cave drawings and engravements evolved into skillful, deliberate expressions, often forming around the suggestive textures of a rock surface and thus recruiting imaginative capabilities characteristic of true art (Morriss-Kay, 2010). Figurines sculpted to resemble human form and drawings depicting geometric patterns and animals, thought to be made during ritualistic ceremonies aimed to summon hunting success, began to explode in production. Additionally, humans began using flat stone slabs as canvases, indicating cognitive development of intuiting artistic potential of unmarked surfaces (Grossberg, 2008; Morriss-Kay, 2010). This capability is thought to have emerged exclusively in *Homo sapiens*. Around 17,000 to 11,000 years ago during the Magdalenian period, archeological data suggests the development of an artistic innovation rate similar to modern day culture (Consoli, 2014; Tylén et al., 2020). From this point onward, art grew as a cultural foundation within premodern societies, with the emerging pressure to seek and create increasingly novel work.

The survival of premodern societies existing during the Magdalenian required constant hunting, gathering, toolmaking, shelter seeking, navigation, disease or wound treatment, and child-rearing. In terms of basic survival, artwork has little functional value; a lack of utilitarianism can be a defining characteristic of artwork (Haselberger, 1961). A cave painting or Venus figurine do not provide any necessary survival resources in of themselves. Additionally, producing artwork is costly in terms of time, mental effort, skill, and materials (Consoli, 2014; Zaidel, 2015). For being seemingly superfluous, art has developed to become an extremely coveted domain in virtually every human culture across the globe (e.g., Langer, 1966; Morriss-Kay, 2010). What was the driving force for the development of artistic skill and expression? From an evolutionary perspective, visual art is primarily a force of social union.

Though painting on cave walls may not directly aid in individual or group survival, being able to vocally express shared symbolism enhances group cohesion, greatly improving the chance of survival. Morriss-Kay (2010) posits that humans have two major biological drives shaped by evolutionary pressure: preservation of the individual and preservation of the social group. As early human groups began to grow in size and complexity, language became necessary in order to promote membership identity and solidarity, which preserves the group as a whole and thus, promotes survival of the individual. Vocal languages began evolving at least 500,000 years ago, with neural circuits underlying symbolic cognition and social intuition developing across various neural regions (Dediu & Levinson, 2013; Zaidel, 2020). Language has since become a significantly prioritized function of the brain, with response to verbal communication starting at notably young ages. According to Zaidel (2020), the evolution of human language co-opted other symbolic systems such as facial expression, body posture, tool-making, and ritualistic, cultural practices including visual art production. The neural pathways that facilitate abstract reasoning, social intuition, and symbolic cognition within language can also apply to other forms of meaningful expression, such as visual symbolism. Thus, the emergence of art can be viewed as an epiphenomenon of language development in humans.

While language greatly promoted social cohesion and conflict resolution in premodern hunter-gatherer groups, the arduous process of group survival amongst changing climates, variable resource availability, bouts of disease, and inter-group conflict put great stress on premodern societies. For a vast period of time encompassing the emergence and rising dominance of *Homo sapiens*, Africa, which is the initial site of human evolution, is thought to have been quite environmentally unstable (Behrensmeyer et al., 2018; Deino et al., 2018). In the midst of struggle, artistry developed as an exaptation of the neural pathways underlying symbolic language development, strengthening group identity and bonding (e.g., Zaidel, 2020). It seems that as members of groups relied on each other for survival and reproduction, unity was an invaluable asset. Both the biological drive to preserve the individual and to preserve the group are reflected in Paleolithic artwork; numerous images of hunting and animals as well as sex, fertility, aggression, and group protective behavior have been found across various parts of the planet. Expanding group culture around the arts was likely particularly effective in promoting bonds between non-kin members of a group, as survival required non-hierarchical dependence between all members. Group identity, or culture, also determined how premodern humans interacted with other groups, as similar identities are more likely to yield social alliances than drastically different ones (Dissanayake, 2000). Hayden (1987) proposed that the emotional evocation of ritualistic artmaking promoted the maintenance of inter-group alliances during periods of scare resource availability. Creating visual artwork also allowed for symbolic preservation against impaired language and social skills within members of a group (e.g., Zaidel, 2014). Interestingly, the production of symbolic artwork does not appear to be as sensitive to brain damage as linguistic functions are, which may account for cases of de novo art production following injury to areas of the brain specialized towards speech and language comprehension (Zaidel, 2014). This use of artwork as a way to overcome linguistic impairment is reflected in modern times by the increased tendency for dyslexic people, who struggle with reading and writing, to develop artistic interest and skill (Kandel, 2012). The arts transcend language in terms of cultural differences as well, as people who do not speak the same language can still experience strong emotions elicited by artwork.

Though the basic cognitive processes recruited during visual art production have been present as part of the anatomically modern human brain for around 200,000-150,000 years (Consoli, 2014; Neubauer et al., 2018), there is a gap of roughly 120,000 years between the emergence of artistic cranial capacity and the widespread cultural prioritization and skill-building of visual artwork. This indicates a period of time that encompassed the gradual, cumulative, and experimental process of developing the skills necessary to create visual artwork. The earliest forms of art are thought to have been collective vocal chorusing and rhythmic movement, recruiting existing sensory-motor traits (Zaidel, 2020). As language developed to encompass modern structure and word precision, proto-art markings became increasingly formed and detailed (Wade & Wade, 2006) as the shared neural circuitry became more efficient. The natural selection of extra-language symbolic practices as a way to ensure group unity promoted increasingly creative, aesthetic, and figurative expressions. This development in artistic skill eventually manifested into the transfer of symbolic meaning into 2D and 3D works of visual art. Morriss-Kay (2010) suggests that the neural development required for modern visual art creation began with the recognition of fossil patterns and uneven surfaces with suggestive silhouettes as being potential canvases. Being artistically inspired by a depression or crack on a cave wall requires the ability to hold a mental image in the mind's eye before and during the process of drawing. Toolmaking, as another extra-language domain, likely promoted the neurobiological development of enhanced motor dexterity, creativity, and visual memory skills, all of which serve as foundational cognitive processes of visual art production. Beginning with basic depictions, the production of drawings, carvings, or sculptures strengthened symbolic comprehension within groups. Over time, visual art became more skillfully and deliberately produced. Elaboration of visual imagery was particularly important in the effective expression of religious beliefs.

As humans gained awareness and complex abstract understanding, we began trying to make sense of concepts outside of the fundamental biological drives necessary for survival, such as the afterlife and origins of creation (Lewis-Williams et al., 2003; Morriss-Kay, 2010). The search for meaning, which is synonymous with symbolic comprehension, significance, and value, emerged as the brain developed, expanding upon its ability to comprehend the basic perceptual features and appropriate responses to the world around us (e.g., Dissanayake, 2000). As neural circuits encoding memory, imagination, and foresight evolved, humans became an active force in the world, using advanced cognition processes to create systemized order. From the ability to make sense of the world emerged culture, which requires the ability to *impose* sense on the world on top of basic survival needs. Culture is guided by symbols or stories to explain who we are and why things are as they are. It promotes group solidarity by arousing collective interest, synchronizing activity, and expressing meaningful messages, which eventually leads to the indoctrination of a set of beliefs and behaviors, also known as religion. Early religious imagery often takes form as human bodies with animal heads, which were marked onto cave walls or sculpted into figurines. These are thought to have been made during shamanistic rituals focused on healing, divination, protection, and afterlife practices (Morriss-Kay, 2010). These ceremonies were likely collective experiences, with evidence indicating that frenzied, trance-like states of minds were reached while creating the art. Human-animal images indicate the development of beliefs concerning spiritual embodiment within premodern cultures. It is thought that the cave walls and other 2D surfaces used as canvases represented the physical barrier between members of a group and the spirit world. There are a number of hand stencils present in cave paintings, such as the hundreds found in Cueva de las Manos (Figure 1). The pigment surrounding the hands pressed against the cave wall was likely blown by a second person, perhaps during ritualistic acts performed to commune with spirits on the "other side" (Lewis-Williams, 2002). The search for meaning and belonging are evolutionarily hardwired across cultures to this day, as art has become an ingrained part of the human experience.

Figure 1. Hand stencils in Argentina's Cueva de las Manos made 13,000-9,500 years ago (public domain photo obtained from Mariano, Wikipedia).

The visual arts have expanded since their prehistoric beginnings as expressions of elemental forces into a force capable of elevating complex social awareness. In order to have lasting sociocultural affects, visual artwork must evoke aesthetic experiences in viewers. As Morriss-Kay wrote, “Art does not exist in a vacuum but requires a social context, otherwise it is meaningless” (2010, p. 173). The human tendency to search for and apply symbolic meaning drives not only visual art production, but also aesthetic evaluation. The ability to aesthetically evaluate artwork is a universal trait among humans, indicating a hardwired evolutionary predisposition. Unlike language, having an emotional response to aesthetic artwork does not need to be learned in order to be experienced. Reacting to aesthetically pleasing objects and faces is present in infants as young as two to three months (Piechowski-Jozwiak et al., 2017), indicating its biological innateness. Shusterman (1997) identified aspects of aesthetic experience as evaluation, phenomenological attention, and the attribution of semantic meaning. These steps rely on introspective functions such as self-awareness and imagination, which are thought to have evolved in part due to pressure on aesthetic experience (Consoli, 2014). The gene-culture evolutionary theory posits that aesthetic evaluation likely stimulated the reorganization of higher-order circuits within the human brain 200,000 to 150,000 years ago, leading to the development of imaginative and intuitive cognition (Consoli, 2014). However, aesthetic experiences in of themselves were initially an exaptation of pre-existing cognitive properties that evolved for other purposes. Evolutionary pressure on aesthetic experiences formed as emotional responses to visual imagery trigger approach-avoid behaviors that are contextually aligned with one’s culture (Shelton, 1992). Aesthetic evaluation of one’s environment and the faces of potential mates led to the evolution of processing beauty as a marker of quality under conditions of honest signaling (Renoult, 2016).

Evaluating beautiful objects, faces, or artwork is emotionally rewarding, activating pleasure circuits within the brain that evolved in order to help us differentiate between cues of attraction and avoidance. Though art is not always emotionally pleasing, aesthetic responses are processed within a reward system (Zaidel, 2016). Rewards evoke positive emotions, which reinforce the behavior that elicited them. Natural and sexual selection pressures shape rewarding or aesthetically pleasing cues as those which promote survival and reproduction. Aesthetically pleasing artwork often captures our attention and evokes pleasure because it portrays shapes, colors, or textures that were ancestrally important to survival or reproduction at some point in time, though the viewer is likely unaware of the biological relevance (Dissanayake, 2000; Stebbing, 2004; Zaidel, 2010). For example, markings that are controlled, fluent, or vibrant are associated with vitality and youth. Bright primary or secondary colors and a glossy or shiny texture signals freshness and health. Jagged lines, sharp angles and the color red may indicate danger, aggression, or violence. The presence of these features in artwork thus elicits different emotional responses within viewers across cultures (Yanulevskaya et al., 2012; Vessel et al., 2019), as they are subliminally associated with useful cues for biological or environmental fitness (Dissanayake, 2000). Because aesthetic preference is shaped by one’s cultural context, having aesthetic experiences in response to visual art has the adaptive function of promoting social bonding, cooperation, and cultural cohesion (Zaidel, 2010; Consoli, 2014).

While making art evolved as a way to solidify group cohesion, it also became a way to differentiate social class (Zaidel, 2010) as agriculture led to stationary demographic expansion during the Neolithic revolution 11,000-5,000 years ago (Klüver, 2008). Division of labor and status led to selective artists producing work individually, rather than as a collective experience. The development of social classes and enhanced skill among dedicated artists led to enhanced artistic ornamentation, which differs from the naturalistic forms previously explored by visual artists (Zaidel, 2010). Often taking a wearable form as jewelry or engraved accessories, ornamentation identified people of high-status. Though wearing or possessing visual art attracted attention from potential mates, being able to make skillful art also became sexually selected for (Consoli, 2014). Displaying one's artwork can be compared to the attention-attraction function of animals' courtship rituals (Zaidel, 2015). Just like a male peacock's tail, making art is costly in terms of time, effort, and lack of utilitarianism. Thus, being a skillful artist would express honest indicators of health, genetic quality, and skills such as dexterity, hand-eye coordination, and motor control (Consoli, 2014; Zaidel, 2015). Over time, artists in certain cultures gained social prestige, further enhancing their reproductive success (Consoli, 2014). It seems that the promotion in cultural prioritization of the arts stems from both the increase in social status of artists and continuation of potentially "artistic" genes via sexual selection as well as the continuation of hedonic aesthetic experiences evoked by artwork as a way to promote bonding via natural selection.

As the Neolithic revolution led to enhanced demographic growth in stationary societies 11,000-5,000 years ago (Bar-Yosef, 1998), knowledge became more far-reaching and long-lasting, as peoples' beliefs, discoveries, and innovations were retained and built upon by successive generations. This is likely the time period in which artistry developed from a social practice to a systemized career. While this spurred technological advancement, seeking creative ways to make visual artwork became increasingly difficult, and thus, rewarding. Evolutionary pressure on creative thinking had already been in place since the development of toolmaking and language, as cognitive flexibility promotes survival via the generation of useful and novel ways to adapt to changing environmental circumstances (Wiggins et al., 2015; Gabora & Kaufman, 2010). Human creativity precedes the innovation of new tools and techniques for more efficient resource gathering, communication, and aesthetically pleasing artwork; creative thinking is thus a product of natural and sexual selection (Gabora & Kaufman, 2010). The Darwinian theory of creativity asserts that the evolution of creative thinking within humans can be thought of as a hereditary process by which ideas are culturally inherited and passed down so that successive generations can build upon preexisting or ancestral ideas (Simonton, 1999; Gabora & Kaufman, 2010). This theory is supported by both creative ideas and genes being inherited over time as cumulative, adaptive, and open-ended processes. Though the ability to generate novel and useful ideas is not exclusively a human ability, the innovative skill of humans surpasses other animals (Zaidel, 2014; Wiggins et al., 2015) due to people sharing ideas and innovations with others, thereby creating a collective pool of information that grows over generation (Dean et al., 2012).

Creativity is defined and promoted by our tendency to seek novelty, a skill that evolved as a way to detect changes in the environment and respond appropriately (Wiggins et al., 2015). Novelty is inherently neutral but is likely to trigger strong emotions ranging from fear to delight as quick responses are vital to navigate sudden change that could be dangerous. Thus, novel and aesthetically pleasing artwork primes some emotional response, even if not a full-blown one (Dissanayake, 2000). However, the hedonic value of novelty is defined by an inverted-U shaped curve, in which too little or too much novelty impedes pleasure by being undistinguishable from ordinary circumstances or completely unrecognizable, neither of which serve as reward cues (Wiggins et al., 2015; Heilman, 2016). The evolutionary pressure for rewarding or pleasing forms of novelty developed in parallel to the development of elaboration, skill, and attention towards visual art forms. Novelty remains a defining characteristic of creativity to this day, with originality ratings of visual artwork being consistent across art experts and nonexperts while other aesthetic qualities such as craftsmanship are not (Hekkert & Van Wieringen, 1996).

Throughout the evolution of modern humans, creativity, visual artwork creation, and aesthetic evaluation served to promote group cohesion, cultural identity, and mate attraction. As cultures gradually developed within communities across the globe, visual art forms did too. The conceptualization, creation, and perception of artwork remain key features of virtually every human culture to this day. Our unique draw towards the arts is biologically hardwired within us regardless of location, time period, culture, age, sex, and race. From a neurobiological point of view, humans must therefore contain brain structures and neural pathways that are complex and multidimensional in their ability to facilitate complex cognitive processes such as abstract symbolic reasoning, self-awareness, novel idea generation, imposition of meaning, and aesthetic experiences.

Neural basis for visual artistry within humans

The modern human brain possesses the capability to facilitate a wide array of complex cognitive and emotional processes. An anatomical prerequisite for this is the remarkable functional capacity of our brain, which has an estimated storage capacity of a quadrillion bytes and 100 billion neurons within the cerebral cortex alone, the outermost layer of the brain responsible for highest-order measures of cognition (Herculano-Houzel, 2009; Bartol et al., 2015). Primates in general have a larger frequency of neurons per volume in the brain and a higher percentage of total brain volume devoted to the cerebral cortex as compared to non-primate mammals (Herculano-Houzel, 2012). The cognitive power of the human brain surpasses that of other primates, as our species departs from the body-brain size relationship found in other primates; the human brain is five to seven times too large for our body size (Herculano-Houzel, 2009). Organization of cortical and subcortical areas within the human brain is different from other primates, allowing for cognitive, social, and emotional processing that is unique to humans in its dynamic complexity (Hrvoj-Mihic et al., 2013). Cortical areas of the human brain also have disproportionate surface area in comparison to brain volume due to cortical folding (Garcia et al., 2018). Though the human brain only accounts for 2% of our body weight, it is the main consumer of glucose within our body, using over 20% of total glucose-derived energy made within the body (Mergenthaler et al., 2013). The brain's energy consumption allows for massive amounts of information processing and computation. Not only do human brains store a remarkable amount of memory and devote massive amounts of energy to computation, but the neural circuits that facilitate such functions also have the capacity to change in response to learning (Hrvoj-Mihic et al., 2013), allowing for environmental events to shape how we respond to stimuli. The cranial and plastic capacity of the human brain allows for complex computation required in the visual arts. Creative idea generation, art production, and aesthetic evaluation all implicate a variety of processes responsible for sensation, memory recall, association construction, reward evaluation, and different types of attentional focus.

The generation of creative ideas or concepts for artwork recruits memory in order to form new semantic connections, which requires executive computation to make sense of and prepare to solve the problem, spontaneous activation of memory construction during incubation periods, and evaluation of ideas or solutions based on their aesthetic or hedonic value (e.g., Bowden et al., 2005). Creative thinking is a product of associative memory, as novel solutions to a problem are formed by integrating remotely related or semantically diverse types of information (Gabora, 2018). Recalling a representation encoded within a specialized cell assembly systematically triggers the retrieval of other representations that share resonant features, thus creating associations between potentially remote memories. Stimuli and events that are encoded in great detail are more likely to overlap in a way that is unconventional, as there are more possible shared features between them that warrant the formation of a creative association, even if they seem completely unrelated (Gabora, 2018). However, the neurons activated during associative memory recall and construction are widely distributed throughout the brain and activity across these cells may be selectively inhibited or recruited by other higher-order structures. In order to strengthen the activation of associations, electrical activity across synapses in regions of the brain responsible for memory construction must be temporally synchronized as determined by Hebbian plasticity. Thus, creative thinking requires unconstrained periods of cognition that facilitate the formation of remote associations as a function of synaptic strengthening that is not inhibited by a more executive state of cognition that directs neural activation across pre-strengthened circuits. Both deliberate and spontaneous processing styles are important in order to stay on task and find a solution to a problem that is useful as well as to allow for non-obvious associations to form (Marron et al., 2018; Henriksen et al., 2020). Additionally, biological reward and salience systems are implicated in the selection of ideas in order to detect ones that are both useful and novel (Oh et al., 2020; de Manzano et al., 2010).

The production of visual art involves focused visual perception of important cues, motor planning, mental imagery, and executive focus on the goal, or end product in mind (e.g., Cohen, 2005; Chakravarty, 2012; Chamberlain et al., 2014; Schlegel et al., 2015). Sensory input from the visual system must be filtered so that only cues relevant to the work being made are being attended to. While making a cave drawing of an animal, for example, one must be focused on the markings being actively made and spaces that will be drawn on rather than areas of the cave wall that are not being used via top-down processing. Focused visual attention must be maintained while one is also using imagination to picture the desired end-product. The goal of getting the externally made markings to align with the internally generated depiction requires visuospatial skill and procedural memory as well as reward processing to evaluate whether a particular line, shadow, or color lines up with the initial idea for the depiction (e.g., Kozbelt, 2001). This problem-solving process requires the selective inhibition of goal-irrelevant material, as creating artwork often requires intense attentional focus (e.g., Chrysikou et al., 2014).

Aesthetic evaluation depends on the resolution of forms within a piece of work that may require executive focus as well as the determination of meaning in relation to both universally common and idiosyncratic schema, thus stimulating reward pathways in our brain that indicate quality (e.g., Kaimal et al., 2017; Vessel et al., 2019). Neural activation stimulated by aesthetic experiences varies based on the content and context of the artwork being viewed (Chamberlain et al., 2014). Aesthetic judgement is often biased by beauty, though not all visual art is meant to be beautiful (Chatterjee, 2011). Evaluation of the aesthetic value of visual artwork is neurally correlated with activation of reward systems within the brain, with rating of beauty being positively related to the degree of activation. Of course, ideals of beauty differ by the viewer's age, culture, education, location, and time period (Chatterjee & Vartanian, 2014; Kandel, 2012). Nonetheless, the universal experience of responding to pleasing objects, faces, and artwork, indicates the vital role of a reward system in aesthetic evaluation. Some styles of visual artwork, such as abstract, cubist, or surrealist paintings, require top-down processing to resolve indeterminate or unclear forms and attribute meaning and aesthetic value (e.g., Cupchik et al., 2009; Pepperell, 2011).

The precise neural bases for visual art production, aesthetic evaluation, and creative idea generation are difficult to examine, as these multi-faceted processes are widely diffused throughout the brain. The content and context of the artwork, as well as individual differences in life events, emotional conditioning, and efficacy of brain functioning affects how the visual arts activate the brain. While the direct anatomical bases of creative thinking, visual art production, and aesthetic evaluation are difficult to pinpoint, all three aspects of the arts require complex interactions between deliberate and spontaneous processing styles with prioritization of rewarding or salient information. Some of these functions, such as executive focus and spontaneous insight, are seemingly contradictory. This indicates a dynamic balance in activation of different areas in the brain that are specialized towards different goals. Creative idea generation, visual art production, and aesthetic evaluation all activate widespread pathways of neurons within the brain (e.g., Ellamil et al., 2012; Jung et al., 2013; Vessel et al., 2019). According to Bressler and Menon, "Although neuronal populations throughout the brain have a variety of different internal circuitry configurations, they can be represented as network nodes if they have a uniquely identifiable local structural organization, a large-scale structural connectivity pattern or a local functional activity pattern that allows them to be distinguished from their neighbors" (2010, p. 278). In other words, networks contain identifiable patterns of activation across neural synapses that may form far-reaching circuits. Using a network paradigm to understand the neural mechanisms of complex cognitive tasks is becoming increasingly relevant as a way to study how regional synaptic connections affect function (Menon and Uddin, 2010).

The role of individual structures or nodes within a single network varies based on the task at hand, allowing for complex integration of percepts, learned concepts, and environmental context in order to solve a problem (Nikolaidis & Barbey, 2018). Some network structures may provide raw sensory input, while some contribute internally generated, conceptual information and others modulate attention or focus between different modes. As a whole, large-scale networks vary in specialization as well: for example, one network may be recruited during the filtered processing of goal-relevant information while another is selectively active while there is no cognitive task at hand (e.g., Fox et al., 2005). Exclusive goal-directed focus, unconstrained association generation, and detection of rewarding or aesthetically pleasing stimuli are all key neurobiological functions that give rise to insight, creation, and evaluation processes of visual artwork (e.g., Bowden et al., 2005; Cupchik et al., 2009; Chatterjee, 2011; Ellamil et al., 2012; Cattaneo et al., 2014; Chrysikou et al., 2014; Vessel et al., 2019). Executive focus, intrinsic and spontaneous simulations, and detection of pleasurable ideas and artworks are respective functions of the central executive network (CEN), default mode network (DMN), and salience network (SN), which are the large-scale brain networks that will be examined in this review. The visual arts require an intricate and unique balance between activation of these networks' functions, stimulating interactions between large-scale brain networks that may not otherwise synchronize (e.g., Ellamil et al., 2012). Research (e.g., Takeuchi et al., 2010; Ellamil et al., 2012; Beaty et al., 2014; Chen et al., 2014; Heilman, 2016) has shown that enhanced creativity, artistry, and aesthetic experiences are correlated with strengthened functional connectivity and increased interactions between these three networks. While the CEN inhibits goal-irrelevant information in order to maintain focus on the task at hand, neuronal assemblies within the DMN facilitate spontaneous memory recall and construction during imaginative, intuitive incubation periods, and the SN computes the salience and emotional valence of visual imagery. The SN is also interconnected with the dopaminergic reward system (DRS), which facilitates the formation of reward cues and feelings of pleasure following artistic engagement.

Even though activation of structures within the CEN, DMN, SN and DRS has been experimentally determined during visual art production, idea generation, and aesthetic evaluation (e.g., Takeuchi et al., 2010; Ellamil et al., 2012; Beaty et al., 2015; Chen et al., 2014), the ways in which the networks interact, and process information differs between the artist and the viewer, particularly during aesthetic evaluation. Past experiences, current goals, emotional conditioning, reward cues, reward sensitivity, memory recall, and brain health or injury all affect the experience that an individual has with the visual arts. Though all people experience art via activation of the CEN, DMN, and SN, the information being activated varies by individual. The viewer is not experiencing the same emotions and memories as the artist, as viewers of a work of art must resolve the meaning of the image by assimilating their own idiosyncratic perspective, a phenomenon known as the beholder's share (e.g., Kandel, 2012). The beholder’s share supports the idea that “art is incomplete without the perceptual and emotional involvement of the viewer” (Kandel, 2012, p. 189).

Artists and non-artists also experience the process of art production and conceptualization differently, with artists having enhanced visuospatial and observational skills and unique strategies of procedural processing while drawing (Kozbelt, 2001; Kozbelt & Seeley, 2007). This variation in perceptual encoding, as well as differences in creative thinking across individuals, may be attributed in part to the synchronization or degree of efficacy in communication between networks according to the network dynamics theory (Eichele et al., 2008; Bolwerk et al., 2014; Nikolaidis et al., 2015; Nikolaidis & Barbey, 2018; Yeshurun et al., 2021). If activation of one network dominates the activity of another due to contrasting processing styles or weakened functional connectivity, it may impair the balance of network functions required for optimal artistic performance. Individual differences in neural function within networks may be due to variations in metabolism, psychological wellbeing, and/or other aspects of brain health (Nikolaidis & Barbey, 2018).

Functional connectivity between the CEN, DMN, and SN varies on an individual basis. Nevertheless, network coupling is a vital neural event during creative, artistic processes within humans (e.g., Ellamil et al., 2012; Beaty et al., 2015). A proposal of this review is that art processes occur via collaboration between large-scale neural networks in order to integrate self-referential, hedonic, affective, semantic, and sensory information. These interactions require a balance between deliberate, spontaneous, and salient processing. This review will focus on large-scale networks encompassing one or more of these types of information and processing styles: the CEN, DMN, and SN. Additionally, the functions of the visual system and DRS will be discussed in relation to artistic engagement. In order to provide context for the visual sensory information being processed within the brain during artistic tasks, the visual system will first be explored. Next, the CEN, DMN, and SN will be discussed independently in relation to the facilitation of creative and artistic processes. The DRS will be explored for its role in facilitating divergent thinking, as well as art therapy and an association between creativity and psychiatric disorder. Finally, the ways in which these systems interact to facilitate visual art idea generation, production, and aesthetic evaluation will be explored, with the proposal of the arts stimulating a distinctive condition of network collaboration. The purpose of this review is to investigate the evolutionary and neural mechanisms by which large-scale networks facilitate creative idea generation, visual art production, and aesthetic evaluation within humans. By doing so, the global prioritization of the visual arts within human cultures and variation in individual experience with artwork will be illuminated as a function of unique coalitions between visual, executive, imaginative, salience and reward systems within the brain.

The Visual System

The visual system provides sensory input that humans are arguably most dependent on (Zimbardo & Ruch, 1975; Kandel et al., 2000). In the visual arts, the importance of the visual system is obvious: in order to create, imagine, and evaluate imagery with intentional lines, shapes, forms, and colors, we must be able to perceive visual input and integrate it with intrinsic information relevant to the task at hand quickly and efficiently. The CEN, DMN, and SN all rely on visual input as a means to evaluate environmental cues for their task-relevant, hedonic value as well as to simulate mental imagery (e.g., Bichot et al., 1996; Kounios et al., 2008; Cupchik et al., 2009; Ardid et al., 2010; Chakravarty, 2012; Gregoriou et al., 2012). The CEN determines the goal-relevance of visual input, the DMN uses visual memory to create new associations and imaginative simulations, and the SN detects visual saliency. Research has highlighted parallelism between the ways in which our nervous systems process visual information and how artists depict imagery (e.g., Stebbing, 2004; Cavanagh, 2005; Kandel, 2016); both use perceptual shortcuts in order to construct visual representations. Projections of light onto the retina within the visual system and the canvas for an artist can both be thought of as two-dimensional surfaces from which the visual system or artist must portray three-dimensional forms via manipulating principles of design such as scale, orientation, and perspective. The role of the visual system in mental imagery, art production, aesthetic evaluation, and the provision of input for motor output will be explored after first discussing the basic pathways by which visual input is processed within the brain.

After photoreceptors within the retinas of the eyes react to light in our environment, electrophysiological signals are transmitted to the brain via the optic nerves (Luo, 2021). Visual input is split by color, line, and motion in parallel pathways that project into the lateral geniculate body within the thalamus. Signals are then sent to the primary visual cortex, which is within the occipital lobe (Kandel, 2012). After reaching the visual cortex, visual input is parallelly transmitted via the dorsal and ventral streams. The dorsal stream carries “where” motion information to the parietal lobes in order for visuospatial processing, while “what” color and line information travels to the temporal lobe via the ventral stream (Mishkin & Ungerleider, 1982; Kandel, 2012; Zaidel, 2016). The dorsal and ventral streams allow for the hierarchical processing and transmission of visual information throughout the occipital, temporal, and frontal cortices (Kandel, 2012). These pathways are critical for effectively perceiving and creating artwork. The inferior temporal cortex (ITC) is where high-level visual processing occurs for “what” information, as the categorization and meaning of objects, faces, and scenes are encoded and resolved in this area (Kandel, 2012; Luo, 2021). As will be discussed later on, visual memory within the ITC and visuospatial information in the parietal lobes is activated within large-scale networks during artistic practices. The visuospatial information transmitted within the dorsal stream allows for effective framing of forms stored within the ventral stream on a canvas or other surface. Damage to the dorsal stream impairs one's ability to localize the canvas or see the scene as a whole (Miller & Hou, 2004). A dysfunctional ventral stream may prevent an artist or viewer from properly identifying an object and thus having an aesthetic response to it. Outside of the arts, injury to these pathways could impair the perception of particular visual features that are transmitted throughout thirty-odd areas of the visual system via parallel pathways specialized towards color, line, and motion (Grossberg, 2008; Kandel, 2012; Zaidel, 2016).

Though visual features are processed in spatially and functionally separate pathways, independent perceptual qualities being processed in areas along the dorsal and ventral pathways are eventually integrated in order to construct visual fields via Gestalt principles (Kandel, 2012). Interestingly, this integration does not happen at a single anatomical site, instead occurring when the activation of the two pathways is coordinated (Treisman, 1996). The construction of objects and scenes is modulated by visual attention, which is directed via shifting one's gaze (Kandel, 2012). Looking directly at objects in one's environment causes them to be selectively attended to via enhanced activation in visual processing cortices that retinotopically correlate with foveal photoreceptors (Luo, 2021). The fovea is an area of the retina with the greatest visual acuity due to its enhanced density of photoreceptors that respond to and recover from light at a specialized rate; this is the center of visual focus (Luo, 2021).

Visual scenes are perceived three-dimensionally, though light projects onto our retina two-dimensionally. A two-dimensional retinal projection could result from any number of differing three-dimensional objects within the visual field which might vary in size, orientation, and distance relative to the viewer (Kandel, 2016). This presents a paradox described as the inverse optics problem. In order to properly interpret visual input, light projections being processed within the brain leads to activation of visual memories acquired via past experiences in order to shape the possible three-dimensionality of the visual cue (Kozbelt & Seeley, 2007; Kandel, 2012). Areas of the brain responsible for high-level visual processing, such as the ITC, compute and test hypotheses for the identification of visual stimuli based on past perception. When perception is led by intrinsically generated information like internally directed attention, expectations, and learned associations, it is top-down (Miller & Cohen, 2001; Kandel, 2016). The hypotheses formed via top-down processing are tested by directing attention towards the most relevant features of a visual cue. Some raw sensory input, also known as bottom-up information, is thus inhibited selectively. Top-down processing thereby allows for appropriate behavioral and cognitive responses to form without having to perceive every feature of a stimulus (Gilbert & Li, 2013), which would significantly slow response time. The CEN and SN use top-down processing on neurons in the visual cortex as they process the relevance of cues towards achieving cognitive tasks or rewards.

Top-down processing is also implicated in aesthetic experience and the beholder’s share in order to attribute meaning to imagery. The results are shaped by memory, which is why looking at artwork evokes responses that may be drastically different between individuals (Kandel, 2016). For example, two people looking at a painting of a feather could have completely different responses. Though both people are likely seeing the feather in a similar way, as the neural mechanisms occurring within their visual systems are the same, the emotional content of the memories or associations with feathers formed by each person over their respective lifetime are obviously different. Interestingly, the presence of certain design principles in visual artwork evoke high ratings across individuals engaged in aesthetic evaluations (Latto & Russel-Duff, 2002). The visual system has evolved to detect and encode contrast, rhythm, balance, and symmetry (Stebbing, 2004), units that are often emphasized in visual artwork (Mendez, 2004). Latto and Russell-Duff (2002) determined that the strongest aesthetic responses to visual artwork occur when the art maximizes initial neural excitation by highlighting one or more of these principles. This is indicative of interactions occurring between the SN and the visual system.

The use of top-down processing within the visual system allows for remarkable flexibility in the brain's ability to resolve visual distortions or physical errors in imagery (Kandel, 2012), which may be intentionally used in schools of art such as Expressionism or Cubism. Artists often emphasize one or a few visual attributes in order to deconstruct and creatively depict an object, a phenomenon known as reductionism (Kandel, 2016). The contours, proportions, shadows, reflections, and colors of objects and imagery within artwork often defy physics of the natural world, using perceptual shortcuts in the brain in order to portray imagery efficiently (Cavanagh, 2005). Schools of art are formed around the use of color or other design elements in a characteristic reductive fashion. For example, Grossberg (2008) points out the lack of lined boundaries within Impressionist paintings; artists such as Matisse often relied on blank spaces between areas of color to be perceived as boundaries within viewers (Figure 2).

Figure 2. Henri Matisse's painting *Les toits de Collioure* (public domain photo obtained from Wikipedia).

The elicitation of emotion is a vital characteristic of visual artwork. One of the most significant ways in which artists do so is through the use of color. We have evolved to associate color hues, tints, tones, and shades with varying emotional and cognitive signals (Dissanayake, 2000). Picasso's Blue Period utilizes the color blue to express and evoke feelings of sadness and loneliness. The bright red sky in Edvard Munch's *The Scream* evokes a sense of unease and danger. Why does color influence emotion so strongly? Color is perceived before other visual features such as form or motion (Kandel, 2012), perhaps because the color pathway contains fewer neuronal projections into the ventral stream and is therefore shorter, potentially decreasing the time it takes for signal transmission to reach the end of the circuit. This indicates that color is an important evolutionary signal for danger, as threats to survival require immediate recognition and emotional perception in order to respond accordingly. The emotions evoked by color are formed by the valence of objects or scenes that contain that particular color (Kaya & Epps, 2004). For example, green is associated with the positive, calming effects of nature while red often evokes feelings of anger or fear as it is the color of blood. Gao et al. (2007) found that the emotional associations of particular colors, such as anger or passion with red, are consistent across cultures. The brightness of colors also impacts mood, with darker colors eliciting negative emotions in contrast to the positive associations of light colors (Boyatzis & Varghese, 1994). Thus, color is one of the most impactful ways to elicit varying emotional responses to a piece of artwork regardless of the viewer's cultural background.

As one practices drawing or painting, special semantic categories for visual information may be created within declarative and procedural memory (Kozbelt, 2001). These categories may be for figural anatomy, how the position of a light source causes shadows to fall on a form, or any number of intersections between features such as space, texture, lighting, color, and lines. Encoding such information into memory allows for more efficient depictions of three-dimensionality via emphasizing or reducing particular features. This process is akin to the inverse optics problem; a three-dimensional object can be represented two-dimensionally by various pairings between size, orientation, and distance. Research (e.g., Rosenblatt & Winner, 1988; Casey et al., 1990) has shown that artists have an enhanced ability to remember complex visual patterns. Glazek (2012) determined that artists shifted their gaze significantly less than novices while drawing from life. Normally, the frequency of gaze shifts is positively correlated with the drawing's accuracy, as constant gaze shifting allows for greater memory retention of relevant features used in comparison as well as the reduction of context effects (Cohen, 2005). The finding that artists had a lower frequency of gaze shifts despite creating more accurate depictions indicates that they were able to process and encode visual input in a quicker and more sustained manner than non-artists (Cohen, 2005). This is likely due to a balance of bottom-up and top-down processing, allowing for nonbiased visual perception as well as strategic encoding of procedural memory.

The specialized visual encoding patterns occurring within the brains of artists also impact motor output efficacy during visual art production. Artists have more efficient perception-to-action processes, with the visual system guiding premotor planning and subsequent coordination of hand movement while drawing or painting in relation to visual attention (Kozbelt, 2001; Glazek, 2012; Chamberlain et al., 2014; Schlegel et al., 2015). Just as visual memory shapes the perception of external and internal stimuli, it also tunes circuits between visual cues and motor movements. Hand movements are encoded within procedural memory, which contains long-term acquisition of knowledge necessary to carry out tasks such as riding a bike or drawing (Kozbelt & Seeley, 2007). As artists learn about spatial features and other properties of objects while drawing them, they develop procedural knowledge of how to analyze and effectively depict the visual world (Kozbelt, 2001). Top-down processing allows one to quickly recognize the lines and shadows making up a form, however, it can also cause fixation on how objects are remembered to appear rather than how they actually appear. In order to prevent habituation of visual attributes, procedural knowledge is thought to be somewhat filtered in artists to prevent it from interfering with the visual accuracy of their work (Kozbelt & Seeley, 2007). The ability to reorient visual perception in order to avoid fixation on how an object is remembered to appear was emphasized by Henri Matisse, who declared, “I don’t paint things. I only paint the difference between things”. Paintings made by Matisse show spatial distortion to indicate peripheral vision or his own hands drawing in his artwork (Pepperell, 2019).

Over time, Western artists have developed reductive and visuospatial techniques that mirror the perceptive shortcuts used by the visual system (Ehrenzweig, 1953). The formation of cognitive strategies used by artists to depict how something appears in an environment rather than how it is remembered to appear is reflected throughout art history beginning in the Medieval period. Work from this era often contains objects that are the same size regardless of distance from the viewer, which looks odd and unnatural. During the Renaissance, artists developed techniques in order to overcome visual perception shortcuts. During the 17th century, painters advanced in their ability to represent shadows and thus, contrast bright areas. Later on, Impressionist painters experimented with the use of unnatural colors, using hues that were conceptually reaching the retina in the external world but were not being perceived due to the brain’s compensation of the colors that should exist rather than those that are actually present (Coney & Bruce, 2004). Finally, Cubism employed the use of several different perspectives of a single object or face compiled together (Ehrenzweig, 1953). Ehrenzweig’s perspective emphasizes similarities between visual artwork and the functional visual system in the construction of images via reductionism. Impairments to the visual system do not necessarily impede one’s ability to make effective and emotionally moving artwork, however (e.g., Trevor-Roper, 1970; Dan, 2003; Zaidel, 2016). Renoir, Cezanne, Picasso, Degas, Rodin, and Matisse are all thought to have dealt with variations of myopia, cataracts, compromised vision due to diabetes, sensitivity to light, retinal degeneration, and other visual dysfunction associated with aging while continuing to actively create artwork. These defects in vision are speculated to have led to characteristic uses of color, fuzzy or unclear contour lines, and contextual lighting (Dan, 2003; Zaidel, 2016).

The visual system is implicated in the internal generation of imagery as well as the perception of external images. Though the mind's eye is creating images internally rather than responding to external input, mental visualization activates the primary visual cortex as well as the ventral and dorsal streams (Mitchison, 1996; Kosslyn et al., 2001; Pearson et al., 2015). This is somewhat unexpected, as creative imaginative simulations form via the formation of novel associations between visual memories stored in higher-order structures such as the ITC. Mitchison (1996) proposed that activity in early visual areas during visualization practices is indicative of feedback pathways originating from the ITC, as if imagining the perception of an image activates the same areas as actual perception. The idea that visualization and perception share the same neural mechanisms is supported by research findings that holding images in one's visual working memory can distort the perception of external stimuli (Kang et al., 2011). For example, imaginary light causes the pupil to adjust accordingly (Laeng & Sulutvedt, 2014). Patients with cerebral achromatopsia, which occurs when the color center of the brain is damaged, lose their ability to perceive color (Lebrecht & Tarr, 2011). Because cerebral achromatopsia is caused by neural injury, it impairs the ability to see color in dreams or mental imagery as well, since imaginative processes share the same neural circuits as external perception. The activation of primary visual areas by mental imagery is much weaker than that caused by actual perception (Pearson et al., 2015). Nevertheless, the vividness of imagery is positively correlated with activation of early visual areas. The higher-order ITC is implicated in the formation of creative visual imagery as well as the evaluation of how effectively internal images resemble previously seen external stimuli (Pearson et al., 2015). In order for mental imagery to form internally, visual input must be encoded in great detail within memory. The retrieval and manipulation of this information will be discussed as a function of the DMN later on.

Visual perception and memory play crucial roles in visual art production, creative idea generation, and aesthetic evaluation. Large-scale networks rely on the visual system for sensory input, but they also manipulate how visual information is processed. Visual perception during artistic tasks is shaped by interactions between the visual system and the CEN, DMN, and SN (e.g., Watanabe, 1992; Bichot et al., 1996; Kozbelt & Seeley, 2007; Bolwerk et al., 2014; Chamberlain et al., 2014; Xu et al., 2020; Yeshurun et al., 2021). These networks are connected to the dorsal and ventral pathways as well as higher-order visual areas associated with memory such as the ITC. Selective inhibition and activation of neurons within visual sensory and memory areas will be discussed as a function of network signaling. The formation of mental imagery, production of artwork, and aesthetic judgement of art require a balance between processing of bottom-up, raw sensory input for analysis as well as top-down resolution of value and goal-directed behavior.

The Central Executive Network

One of the most crucial brain networks in facilitating artistic creativity is the CEN. The CEN is a frontoparietal system (Figure 3) containing the prefrontal, posterior parietal, and anterior cingulate cortices (Miller & Cohen, 2001). It facilitates higher-order brain functions such as self-awareness, symbolic conceptualization, abstract reasoning, planning, decision-making, and problem-solving (Miller & Cohen, 2001; Chakravarty, 2012; Teffer &

Semendeferi, 2012; de Souza et al., 2014). The CEN regulates externally directed attention on such tasks while using top-down processing to filter multimodal information by its relevancy to one's goals and past experiences (Miller, 2000; Beaty et al., 2015). The extensive connectivity of this network to other cortices allows for the selective inhibition or recruitment of activation across neural assemblies responsible for processing memory, emotion, motor movement, and sensation (Siddiqui et al., 2008; Beaty et al., 2015). Activated information is then manipulated in working memory, which requires executive focus on the problem at hand. Whether it's for the selection of a particular design sketch, the execution of a painting or sculpture, or the process of figuring out the symbolism of a work of art that one is viewing, executive focus allows artists and viewers to successfully complete their goal. The CEN provides the computational capacity necessary to manipulate mental imagery, form relational associations, and maintain focus on a goal, all of which are necessary processes within the visual arts.

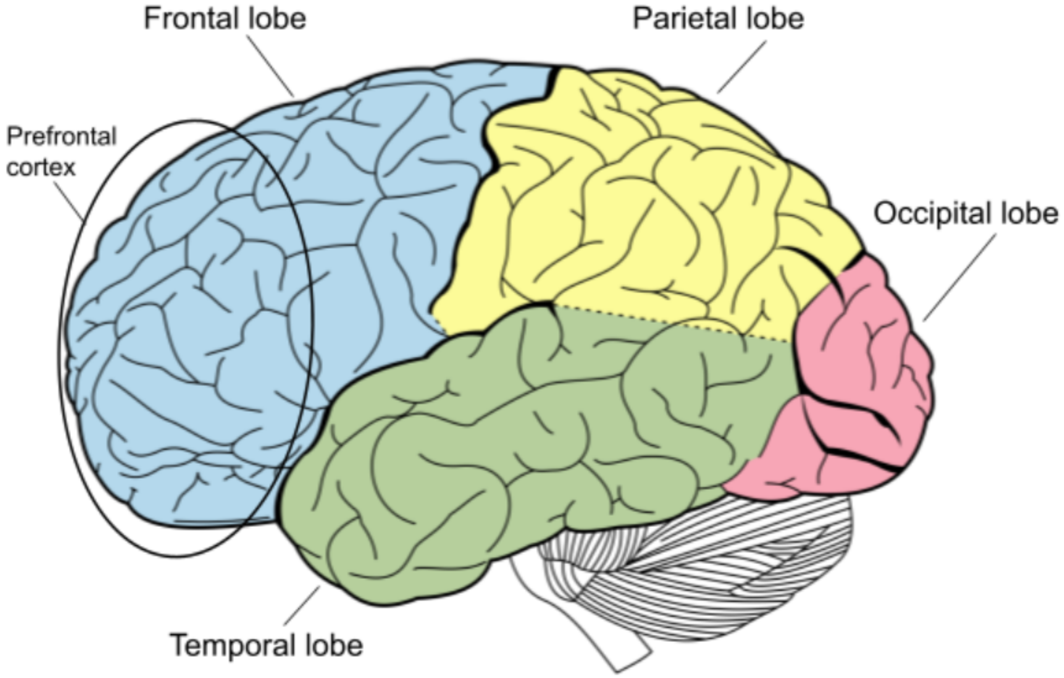

Figure 3. Cortical anatomy of the human brain in lateral view (public domain photo obtained from Henry Vandyke Carter with alterations by Mysid, Wikipedia).

Humans emerged as a dominant species due in large part to an increased intelligence and capability to perform complex tasks requiring cognitive control (Miller & Cohen, 2001; Lakatos & Janka, 2008). Cognitive control is the ability to consciously act in alignment with our complex and long-term goals rather than react reflexively or habitually towards what is directly in our environment in a given moment (Miller, 2000; Beer et al., 2004). Being able to executively focus on long-term goal attainment allows for navigation of multi-faceted social settings and rapidly changing, unpredictable environments. Cognitive control requires effective storage, recall, analysis, and integration of various forms of information from all over the brain, often in a parallel fashion. This advanced computation primarily emerges from a core hub of the CEN, the prefrontal cortex (PFC) (Miller, 2001; Ellamil et al., 2012). The PFC hierarchically receives, processes, and integrates various types of input from lower-order structures that it integrates in order to compute appropriate behavior for a given situation or task (Miller, 2000). This cortex evolved in hominids around 30-19 million years ago and underwent significant expansion as human species developed (Smaers et al., 2017). The PFC as a whole is disproportionately larger in humans than in non-human primates, making up a third of the cerebral cortex (Siddiqui et al., 2008; Glasser et al., 2014; Donahue et al., 2018). The expansion of the PFC during the evolution of modern humans likely facilitated the development of language and extra-language circuits (Deacon, 1997), which were later co-opted for the creation of visual art (Zaidel, 2013). Along with its disproportionate size, the human PFC contains neurons in with greater synaptic spine density and dendritic branch complexity than those in sensory and motor cortices (Bianchi et al., 2013). This hyperconnectivity allows for input from various sensory, premotor, and limbic areas in the brain to reach relatively local executive circuitry. Furthermore, the gene THBS4, which encodes the thrombospondin protein responsible for regulating synaptogenesis, is expressed at a higher level in the human PFC relative to other primate species (Cáceres et al., 2007). The spatial complexity and plastic potential of the PFC, along with the numerous modes of sensation that are transmitted to this cortex, allow for greater neural plasticity and integrative function (Siddiqui et al., 2008). Plasticity is a crucial component of creativity, as novel ideas spur from the formation of new semantic associations via synaptogenesis.

The main structures within the CEN are the prefrontal cortex (PFC), posterior parietal cortex (PPC), and anterior cingulate cortex (ACC). The PFC regulates cognitive control and highest-order processing (Miller, 2000; Beer et al., 2004). The PPC is implicated in visuospatial skill, as it processes bottom-up visual input and manipulates goal-relevant cues in working memory via top-down processing (Shomstein, 2012). Finally, the ACC modulates attentional control over primary sensory input and resolves cognitive conflict within the CEN (Miller & Cohen, 2001; Crottaz-Herbette & Menon, 2006). Neural circuits within the ACC respond to the simultaneous activation of incongruent pathways within the CEN and resolve conflict via allocating control towards the more salient input. The function of structures within the CEN are all carried out via a top-down processing style that filters information within the brain. To maintain focus on goal achievement when there are large amounts of multimodal sensory input competing for attention, the brain must be able to modulate internally and externally generated information so that only the most relevant stimuli reach awareness (Xu et al., 2020). This filtering system is modulated by sensory gating, which occurs when neurons suppress inputs created by stimuli that have been previously deemed as irrelevant, causing latent inhibition of unnecessary information (McCormick & Bal, 1994). Sensory gating, or latent inhibition, is initiated by presynaptic filters that form in response to neurotransmitter release at particular times within a behavioral sequence, suppressing irrelevant incoming information (Bamford et al., 2018). Without latent inhibition, cortical brain centers would be flooded with information, exhausting attentional resources. The PFC modulates attention towards neural circuits containing task-relevant information by sending excitatory signals to interconnected brain systems (Desimone & Duncan, 1995; Miller, 2000). This executive focus is an important asset in the evaluation of creative ideas and nonrepresentational artwork, as meaningful analysis of abstract internal or external symbolism may require high concentration (Miller, 2000; de Souza et al., 2014).

The PFC is activated by a variety of artistic practices that require cognitive control (e.g., Cela-Conde et al., 2004; Cupchik et al., 2009; Kowatari et al., 2009; Chakravarty, 2012; de Souza et al., 2014). The PFC is structured into hierarchical subregions in order to organize the wide range of functions this area of the brain is responsible for (Miller, 2000; Siddiqui et al., 2008). Anterior regions of the PFC are active during significantly abstract processing. The rostral PFC contains circuitry responsible for comparison and association of different semantic categories (Gonen-Yaacovi et al., 2013; de Souza et al., 2014). Caudal regions of the PFC are highly interconnected with the amygdala and other limbic structures (Barbas, 2000) and are thus involved in emotional and reward processing. Perhaps the most vital subunit of the PFC in facilitating artistic output, however, is the lateral PFC (Gonen-Yaacovi et al., 2013). Lateral PFC neurons encode associations between external events, internal states, and actions required to solve a problem or goal (Miller, 2000). This subregion is specialized towards analysis of task contingencies as it is directly interconnected with sensory, motor, and limbic cortices responsible for reward. Coming up with a novel and useful idea for a piece of artwork, making said artwork, and being able to figure out what a painting means symbolically and figuratively are all goals; the lateral PFC is directly involved in the execution of all of these processes. For example, viewing a bold brushstroke that one has just made across a canvas activates different neuronal ensembles depending on whether or not it makes the painting more closely match the internal goal or image in mind. This initial activation spreads to associated pathways that one has made over their lifetime (Miller, 2000), recruiting relevant information from memory, sensory, and limbic areas of the brain in order to form a bridge between the event that had just occurred and what to do next in order to obtain the goal. Task-contingent associations between visual input, internal states, and reward attainment may not form immediately, however, as neuronal circuits within the PFC have the ability to sustain a short-term buffering period to allow for working memory information to be analyzed effectively (Fuster et al., 2000; Miller & Cohen, 2001). This temporal flexibility allows for focus to be maintained on goal-relevant information, such as whether the texture or color of the brushstroke aids in the depiction of a certain form, even as an individual momentarily pauses in order to internally reflect. Once the appropriate response has been computed, e.g., thickening the brushstroke or making the color duller, it is executively imparted to various regions of the brain such as the supplementary motor area (SMA) (Miller, 2000; Koechlin et al., 2003; Siddiqui et al., 2008). The SMA is a premotor region that integrates external information (visual cues) and internal states (goal associations) in order to plan motor action (Nachev et al., 2008). The integrations formed by SMA corticospinal cells are directly transmitted to motor neurons to activate the planned movement.

As one practices attaining goals within a similar domain, such as the execution of a painting, reward signaling cues are recognized more and more efficiently as past experiences of goal attainment strengthen task-contingent associations (Watanabe, 1992). Lateral PFC neurons can tune the encoding specialization of visual neurons as task-contingent associations strengthen, causing cells in the visual cortex to gain sensitivity to goal-relevant stimuli regardless of their initial encoding specialization (Bichot et al., 1996). By increasing the firing rate and coding efficiency of visual neurons following exposure to task-relevant stimuli, the lateral PFC uses top-down control to modulate attention towards a particular attribute (Ardid et al., 2010). Selective increases in visual neuron sensitivity may be why artists are able to analyze object and image structure more efficiently than non-artists

(Kozbelt, 2001). The lateral PFC is able to enhance visuospatial observation and evaluation, and damage to this cortex may cause artistic composition and depiction to suffer (de Souza et al., 2014).

The ability to activate visual neurons covertly and selectively is a function of the PPC as well as the PFC (Ardid et al., 2010; Xu et al., 2020). For visual art production, visuospatial input and manipulation are extremely important for the depiction of three-dimensional forms on two-dimensional surfaces, particularly when drawing from observation. Observational drawing requires executive focus on particular features of a person, landscape, or object in order to effectively depict its likeness while suppressing irrelevant aspects of the visual field. The PPC contributes to visuospatial skill because it contains neurons that project into the dorsal stream, which transmits "where" visual information (Chakravarty, 2012; Hebart & Hesselmann, 2012; Rehman & Khalili, 2022). The PPC processes bottom-up signals from the dorsal stream and elicits attentional shifts towards relevant cues that can be manipulated via top-down processing the PFC (Buschman & Miller, 2007; Shomstein, 2012). Synchronization between the PPC and PFC regulates how attention is directed towards visual cues. When visuospatial working memory is being activated by artistic tasks, alpha synchronization is witnessed in the PPC. Alpha waves are measured in cortical areas between 8-12 Hz when one is relaxed, or selectively inhibiting brain activity in order to form remote associations, mental imagery, or to manipulate working memory (von Stein & Sarnthein, 2000). Alpha activity within the PPC during visuospatial tasks indicates internal attentional control over what features are ignored, and which receive the most attention (Sauseng et al., 2005; Fink et al., 2009).

Patients with damage to the right PPC commonly suffer a loss of artistic ability (Miller, 2008; Chakravarty, 2012). This indicates involvement of PPC neurons during artistic tasks that require visuospatial skill (Schlegel et al., 2015). However, professional artists show less activity in the parietal cortex than non-artists while in the process of designing (Solso, 2000; Miller, 2008; Kowatari et al., 2009). This may be because the processing of visuospatial features in artists is more efficient than in non-artists and thus requires lower levels of activation. While artistic training in observational drawing is not correlated with higher activation or structural changes in the PPC, it is linked to an increase in gray matter within the SMA (Chamberlain et al., 2014). Because the connections from the SMA to the primary motor cortex are reciprocal, an increase in gray matter within the SMA is correlated with superior proprioceptive feedback and hand-eye coordination that allows for artistic replication of visual features (Nachev et al., 2008). Recall that as one develops their artistic skill, the cognitive strategies by which visual input is processed change (Kozbelt, 2001). One such strategy may be the deconstruction of an object's general spatial identity into its abstract, local features in order to prevent procedural memory from impeding accurate depiction (Kozbelt & Seeley, 2007). This process may contribute to artists having less PPC activation than non-artists while drawing, as the top-down manipulation of visuospatial input is being suppressed.

Top-down processing: help or hindrance to artistic engagement?

Though the CEN's ability to impart top-down control on various brain regions allows for the efficient selection of relevant information from memory, sensory, affective, and motor cortices, top-down processing may not always benefit artistry. Bottom-up visual input is important in the evaluation and depiction of form, and latent inhibition evoked buy the CEN may impair an artist's ability to accurately depict something (Glazek, 2012). Similarly, top-down processing may impair the formation of creative semantic combinations during idea generation, as distant, weakly activated associations may be unconsciously deemed as irrelevant, preventing them from forming under executive control (Bowden et al., 2007; Fink et al., 2009). Thus, creativity is often generated when inhibition of seemingly remote or irrelevant information dissipates while solving a problem, allowing novel relationships between domains to form. This supports the idea that creativity is facilitated by a lack of filtration evoked by the CEN.

The positive effect of absent CEN censorship on visual artistry is illustrated by looking at case studies of frontotemporal dementia (FTD). FTD arises from the bilateral atrophy of the frontal lobes, anterior temporal cortex (ATC), and ACC (de Souza et al., 2014). While degeneration of the PFC and regions of the temporal cortex would seemingly impair artistic abilities due to the involvement of these areas in artistic evaluation and production, numerous case studies report an increase in artistic skill and creativity following early FTD progression in individuals (Mendez, 2004; Miller & Hou, 2004; de Souza et al., 2014). It is estimated that around 10% of FTD patients who experience selective degeneration of the temporal cortex gain compulsive artistic tendencies despite a lack of prior art interest or experience (Miller et al., 1996). This is surprising, as most forms of dementia are associated with a decline in artistry, particularly in visuospatial relationships. This phenomenon is therefore an example of paradoxical functional facilitation, a term denoting unexpected improvement in artistic performance such as drawing following neurodegeneration (Kapur, 1996). It is thought that artistic interest may grow following frontotemporal degeneration because top-down inhibitory mechanisms emerging from the PFC and ATC and projecting onto the posterior temporal cortex and PPC are eliminated due to neuronal degradation (de Souza et al., 2014) As the posterior temporal and parietal cortices are responsible for visuospatial processing, a lack of inhibition on these regions could lead to the improvement in realistic or surrealistic depictions made by FTD patients (Miller & Hou, 2004). Damage to the ATC in particular is associated with heightened visual awareness, as this area is thought to suppress input from the visual cortex (Miller et al., 1996). This is demonstrated by a case in which a man who began showing symptoms of FTD such as increased visual sensitivity, verbal repetition, and disinhibition, experienced a flourish in creativity and artistic skill. Degeneration was relatively limited to the ATC; paintings were based on enhanced light and sound experienced from the environment (Miller et al., 1996).

Despite commonly impairing verbal skills, individuals diagnosed with FTD often find a passion for painting, even going on to win awards and recognition for their work (Mendez, 2004). Such an increase in artistic skill in FTD patients may be driven compulsively, with repetitive practice leading to the relatively quick progression of talent. Interestingly, FTD patients often recreate visual scenes or objects remembered from childhood despite impairment in semantic memory (Mendez, 2004). Such paintings may possess more impressionistic and emotional stylization, even as language and other executive skills become increasingly dysfunctional (Mell et al., 2003; Mendez, 2004). Examining de novo art production in FTD patients demonstrates that while creating artwork relies on activation of executive parietofrontal regions, creativity remains a widely diffused function of the brain that may be enhanced by a lack of filtration.

The effects of CEN censorship of creativity can be examined within individuals who have not undergone neurodegeneration as well (e.g., Radel et al., 2015). The generation of highly original and useful ideas is associated with an increase in alpha synchronization within the PFC, with the magnitude of originality and synchronization being positively correlated (Grabner et al., 2007; Fink et al., 2009). While this finding and FTD case studies support the idea that top-down processing or latent inhibition emerging from CEN neurons may impair creativity and visual art production, these processes also require some level of filtration in order to get done. Attaining goals that require cognitive control require some degree of filtration in order to prevent irrelevant information from pulling at one's focus. In order to effectively understand a task and evaluate the appropriate cognitive or behavioral response requires an analytic and executive processing style in order to maintain focus on goal-relevant task details (Zabelina, 2018). Chrysikou et al. (2014) proposed a matched filter hypothesis of cognitive control theorizing that executive control leads to optimized performance on tasks that are goal-directed, conceptually abstract, and require manipulation of external representations. As all of these features are important in artistry, the matched filter hypothesis supports why activation of the CEN has been positively associated with artistic production.

Activation of the CEN is crucial in the evaluation of abstract artwork. Kandel (2016) wrote that abstract visual art is created to stimulate recall and assimilation of memories and emotions specific to the viewer, rather than to depict a clear and detailed form. Though abstract artwork promotes personal involvement in the attribution of meaning, it also often contains visually indeterminate imagery. Visual indeterminacy occurs when one is unable to identify or attribute meaning easily to a seemingly familiar visual stimulus (Pepperell, 2011).

Processing visually indeterminate artwork causes the visual perceptual features to become separated from the semantic aspects, making it difficult to evaluate the aesthetic value of a work of art (Ishai et al., 2007). Recall that the visual system requires top-down processing in order to recognize the identity and subsequent affective and semantic associations of an image (Kandel, 2012), and that this is led by previously attained visual prototypes, which are referential composites of the most salient features within a category such as ‘tree’ or ‘man’ (e.g., Dahlman et al., 2016). Thus, visual determination is most effective when the image in question contains certain features that are representative of a particular category. However, creations made by Impressionistic, Surrealist, and other abstract artists often contain nonrepresentational imagery that lacks defining features (Vessel et al., 2019).

Visual indeterminacy is often intentionally used by artists in order to stimulate the beholder’s share (Pepperell, 2011). Often, the degree of ambiguity within a piece of artwork corresponds to demand placed upon the beholder’s share; thus, abstract artwork involves cognitive control more than figurative artwork. Additionally, there is a positive relationship between the amount of time and effort necessary to comprehend a visual image and the strength of aesthetic rating subsequently attributed to it (Ishai et al., 2007). Thus, engagement of the viewer’s attention and imagination stimulated by abstract visual artwork may lead to a more aesthetically pleasing or emotional experience viewing said artwork. Monet was known to call upon the beholder’s share through the depiction of light in his paintings, much as Kandinsky created objectless or indeterminate geometric images in order to evoke a more personal comprehension and evaluation of his work (Figure 4) (Pepperell, 2011)**.** Soft edges, manipulation of characteristic features, and primitive forms are often used to create nonrepresentational images that stimulate top-down processing. Viewing abstract artwork activates the brain more broadly than figurative artwork does (Kawabata & Zeki, 2004), involving wide-spread collaboration facilitated by the CEN between sensory cortices and emotion and memory cortices in order to resolve visual and meaningful evaluation of the art.

Figure 4. Wassily Kandinsky's painting *Composition VI* requires top-down processing during aesthetic evaluation (public domain photo obtained from WikiArt).

Aesthetic evaluation of ambiguous or visually indeterminate artwork strongly activates the ACC (Kirk et al., 2009), as this region regulates attentional control in dynamic problems that do not have a single correct solution (Walton et al., 2007). The ACC is also implicated in emotional regulation (Etkin et al., 2011), with the emotional content of a visual image influencing how ACC neurons direct attention towards it (Braem et al., 2017). While the ACC is activated by aesthetic evaluation regardless of subsequent judgement, the lateral

PFC and PPC are recruited primarily by aesthetically beautiful objects (Cela-Conde et al., 2004; Cattaneo et al., 2014). Aesthetic experience stimulates image construction and visuospatial exploration of stimuli in order to resolve forms, recruiting the PPC, while the lateral PFC is activated in order to maintain focus on the most goal-relevant visual features (Cupchik et al., 2009; Cattaneo et al., 2014). Visual information within the ventral stream, which encodes "what" features, is transmitted to the lateral PFC for identity resolution (Gilbert and Li, 2013). The lateral PFC which uses top-down processing to sort object stimuli into functional categories in order to resolve the probable identity of an object (Kandel, 2012). Viewing artwork in an actively appreciative and subjective way rather than from a detached, objective perspective leads to greater activation of the lateral PFC (Cupchik et al., 2009). Attention thus affects aesthetic evaluation and requires some measure of cognitive control facilitated by structures within the CEN (Höfel & Jacobsen, 2007). A viewer cannot simply concentrate on only the most eye-catching features within a piece of artwork in order to fully understand the painting as a whole, however. Taylor et al. (2011) found that efficient analysis of abstract work stimulates a broad, even gaze over a canvas rather than a focal, converging gaze that tracks only the most salient features.

Creative idea evaluation, art production, and aesthetic evaluation all require some level of cognitive control that is facilitated by the CEN. While latent inhibition of information that is irrelevant to the goal allows for efficient execution of artistic processes, high levels of censorship can impair one's creativity, which impacts the formation of unconventional ideas and the interpretation of complex or ambiguous visual artwork. CEN filtration during artistic processes is modulated by interactions with other networks such as the DMN.

The Default Mode Network

While top-down control emerging from the CEN maintains focus for goal attainment, creative insight and idea generation are related to activation within structures of the DMN (Ellamil et al., 2012). The DMN is active in the absence of external attention and facilitates the processing of intrinsic information relative to the self and others, thereby generating self-awareness, social intuition, empathy, and creative insight (Buckner et al., 2008). Insight can be defined as the sudden awareness of a solution to a problem with no preceding conscious processing (Metcalfe, 1986; Kounios et al., 2008; Ellamil et al., 2012). These spontaneous realizations are often referred to "Aha!" moments, which have been attributed to some of the most significant creative and scientific discoveries throughout history (Metcalfe & Wiebe, 1987). Though insight is difficult to experimentally study, neural activity within regions of the DMN such as the medial PFC, posterior cingulate cortex (PCC), precuneus, and medial temporal cortex (MTC) has been observed in correlation with self-reported "Aha!" moments (Bowden et al., 2005).

Neural circuits within the DMN are activated in the absence of externally oriented attention or focused cognitive effort, and generate imaginative scenarios designed to process introspective or social concerns (Buckner et al., 2008). The DMN is often considered task-negative since it is deactivated during cognitive tasks, and the degree of deactivation within certain regions of the DMN has been positively correlated with task performance (Eichele et al., 2008). However, it is not entirely accurate to characterize the DMN as task-negative because it is recruited during insightful problem-solving that relies on internally generated information and social intuition (Raichle et al., 2001; Fox et al., 2005; Andrews-Hanna et al., 2014). The DMN not only passively facilitates the reconstruction of past experiences, but also forms new associations. Buckner et al. posited that the primary function of the DMN is to “simulate an alternate perspective to the present” by recalling memories and making connections from the past to the present, as well as visualizing future possibilities (2008 p. 23). Humans are thought to reflect on personal experiences, intuit the inner lives of others, mentally time travel, and imagine fictitious scenarios with much greater frequency than other animals (Suddendorf & Corballis, 2007). It is estimated that 30-50% of our waking cognition is directed towards mind-wandering, which is the passive shift in attention away from task-relevant stimuli towards internally generated information (Klinger & Cox, 1987; Andrews-Hanna et al., 2014). Though non-human primates and some non-primate mammals have systems that are broadly functionally analogous to the DMN in humans (Mantini et al., 2011; Lu et al., 2012), there are anatomical differences that suggest that variations in the functional connectivity between structures of the DMN between humans and nonhuman primates differs as a function of social network size (Mars et al., 2012). Because creating and experiencing an emotional reaction to visual art requires introspection and emotional intelligence, the advanced function of the DMN within humans is likely why we are the only species that is continually and consciously drawn to the arts.

In humans, the ability to use imagination to solve problems is thought to originate from the need to understand the inner thoughts and emotions of other people within one’s social group (Mars et al., 2012). As an incredibly social species, humans possess unique abilities to understand the inner lives of others by interpretating emotional and behavioral variations in others’ facial expressions, body postures, et cetera (Saxe, 2006). The capacity to attribute mental states to others is known as theory of mind (Premack & Woodruff, 1978), and it allows us to anticipate the motives of others, manipulate behavior, and keep track of social dynamics between group members, all of which contribute to ensuring one's place within the group, thus increasing the probability of survival and reproduction (Mars et al., 2012). The social brain hypothesis speculates that the enlarged size of the primate brain relative to non-primate organisms evolved in order to generate the cognitive and behavioral complexity necessary to navigate living within social groups (Dunbar, 1998). Anatomical changes observed during the evolution of the human brain point to the idea that expanding imaginative abilities by enlarging regions of the DMN was a prerequisite to the development of creative innovation and social intuition seen in modern humans (Carroll, 2020). For example, a significant increase in the surface area of inner parietal areas such as the precuneus occurred as modern *Homo sapiens* developed (Neubauer et al., 2018). The precuneus is one of the major regions within the DMN, and facilitates internally generated information such as visual imagery, self-awareness, and social intuition. Being able to intuit someone else's perspective, feel social acceptance and/or rejection, and respond appropriately is a crucial precondition to surviving within social groups (Mars et al., 2012). Such perspective-taking requires internal reflection and conceptualization as well as efficient memory encoding and retrieval. Internally generated emotions, beliefs, and conditional responses must be integrated with incoming sensory input and relevant memories in order to consistently contextualize and understand the constantly changing social environment (Yeshurun et al., 2021). This intrinsic recall and reconstruction is facilitated by activation of the DMN, which occurs during conditions of mental rest or while passively viewing a stimulus (Raichle et al., 2001; Ellamil et al., 2012). The significance of the DMN in social development has been highlighted in functional near-infrared spectroscopy (fNIRS) studies that show synchronized neural firing patterns within the same regions of the DMN of caregivers and children whilst communicating (Yeshurun et al., 2021). This coupling is likely representative of a shared semantic understanding that is involved in the social development of language and learning.

Major nodes of the DMN such as the precuneus, medial PFC, MTC, and PCC are spatially distanced so that connectivity to major structural modules of the brain is present, leading to multiple types of data converging onto the network (Hagmann et al., 2008). Incoming extrinsic information is thus integrated with intrinsic information based on its content, not its sensory modality (Yeshurun et al., 2021). Margulies et al. (2016) proposed that the DMN exists at the end of a spectrum that encompasses direct perception and action on one end and abstract cognitive processes on the other. The spatial dimensions of this network, along with its extensive connectivity to major cortical structures, give rise to the idea that the DMN is critical for generating abstract representations of one's cognitive landscape. The functional efficiency of the DMN can be attributed to it being composed of multiple, specialized subnetworks (Andrews-Hanna et al., 2010; Buckner & DiNicola, 2019). The PCC is thought to function as an interface between distinct networks involved in the DMN (Leech et al., 2011), regulating attention between different structures such as the MTC memory system and dorsal medial PFC system, which is engaged in regulating self-awareness (Andrews-Hanna et al., 2010). The various structures and specializations involved in the DMN allow for multi-faceted integrations to be executed in order to keep track of complex, long-term group dynamics and effectively evaluate the aesthetic value of visual images. Impaired social and imaginative capabilities, which are commonly observed in individuals with autism spectrum disorder (ASD), is often attributed to a lack of connectivity between regions in the DMN such as the medial PFC and PCC (Li et al., 2014), leading to difficulty in comprehending facial expressions and regulating self-awareness of one's own emotions (Wager et al., 2008; Ebner et al., 2012). Dysfunction within the DMN may explain why artistic ASD savants often draw hyper-realistically, with little emotional or abstract expression (Drake & Winner, 2009) as creative insight processes are impaired.

Insight is not a unitary process in of itself; it is the result of multiple neural and cognitive events occurring in a variety of domains (Bowden & Jung-Beeman, 2007). The mechanisms of insightful problem-solving are different from the highly goal-directed, filtered processes by which the CEN facilitates art production and evaluation. While the CEN generates filters in rule-driven manner, insight arises when filtration of seemingly irrelevant information ceases during automatic processing, allowing weakly activated, non-obvious representations to reach consciousness (Bowden et al., 2005). A diffuse processing style and lack of executive censorship facilitate creative insight in alignment with Gestalt principles, as one's perception of a problem is restructured from its individual features to the total relations between them (Haavold & Sriraman, 2021). The effect of these conditions on promoting insight can be understood by examining activation of visual processing areas under conditions that recruit the DMN. Individuals who have a tendency to solve problems via insight rather than by using executive strategies show greater activation across different specializations of neurons within the visual cortex (Kounios et al., 2008). Such broad activation allows for non-attended sensory information to be processed within the DMN when the environment is being viewed passively rather than inhibited by dominant focus on more relevant cues. Insightful problem-solving mediated by activation of the DMN can thereby lead to more novel and unconventional ideas for art projects than the analytic processing style of the CEN can, as remotely associated information is being spontaneously processed. According to Bowden et al. (2005), insight occurs when the introduction of a problem activates remotely associated information while simultaneously not activating strongly relevant information. People are able to generate more creative ideas to solve a problem when they are unaware of what type of solutions are typically applicable (Finke, 1996). This is because focusing on conventional solution categories impairs the ability to come up with nonconforming and imaginative ideas. By activating remote semantic networks instead of conventional ones, non-biased and unconventional interpretations are integrated until signals become strong enough to reach consciousness (Bowden et al., 2005). Bowden et al. also posits that the inhibition of solution-relevant information at the initiation of problem-solving only occurs if one purposefully decides not to consciously brainstorm. Exerting high levels of focus on problem-solving can hinder the ability to come up with creative solutions as it activates the CEN and subsequently, filtration via sensory gating. Conversely, purposefully distracting oneself or promoting mind-wandering is positively correlated with creative insight (Dijksterhuis & Meurs, 2006). The length of the incubation period, or amount of time one spends deliberately mind-wandering after the introduction of a problem, is directly related to the generation of highly original ideas (Baird et al., 2012; Agnoli et al., 2018). Defocused attention allows for events and schemas to be processed more broadly and in greater detail, thereby increasing the possible associations that can be made. In the absence of selective attention, sensory gating is lessened. Thus, incoming sensory information and semantic representations are able to be processed and combined more elaborately. Reductions in latent inhibition via the loosening of sensory gating mechanisms are observed to be greater in people who are high creative achievers as compared to low creative individuals (Carson et al., 2003). Such highly creative people are able to produce original ideas for artwork through neural integration of internally and externally generated information that is retrieved from remote, wide-scale neural networks.

Along with creative insight, the DMN facilitates aesthetic evaluation, which also promotes one's place within a group. Recall the evolutionary purpose of aesthetic experience in determining object and mate quality, as well as allowing for participation in a society's distinct cultural and artistic style. Aesthetic experience heavily involves DMN structures associated with emotional introspection, empathy, and self-awareness, as these functions are critical for engagement of meaning processes involved in the perception of visual artwork (Vessel et al., 2019). As people view painted portraits, they unconsciously change their facial expression to mirror the subject, demonstrating the role of social intuition in aesthetic evaluation (Kandel, 2012). Though the DMN is typically disengaged when one is focusing on the external environment, this network is highly activated while evaluating visual artwork that is aesthetically appealing. The medial PFC, precuneus, and temporoparietal junction are all activated during aesthetic evaluation (Zaidel, 2016), with the magnitude of neural transmission directly correlating to the strength of aesthetic appeal of a visual image (Kaimal et al., 2017; Vessel et al., 2019). Vessel et al. (2019) determined that DMN engagement facilitates aesthetic appeal regardless of what type of art is being (for example, abstract versus figurative). The DMN is engaged by portraits, landscapes, and architecture despite these visual scenes containing distinct perceptual codes. This suggests that the DMN is involved in integrating non-perceptual aspects of aesthetic experience such as internally generated emotion and self-referencing with the visual features of a piece of art (Vessel et al., 2019). As the diverse schemas and intrinsic beliefs acquired by an individual shape the circuits formed within the DMN, anatomical variations of the DMN between humans account for differing individual interpretations of artwork (Yeshurun et al., 2021). Activation of the DMN during aesthetic evaluation is not necessarily present for abstract works of visual art, as making sense of nonrepresentational imagery requires top-down processing, which is facilitated by the CEN.

The specific hubs of the DMN involved in integrating intrinsic and extrinsic information are the MTC, temporoparietal junction (TPJ), and precuneus (Raichle, 2001). Under rest conditions, spontaneous MTC activation in humans has been linked to the unsolicited re-activation of recent memories and excitation of neuronal ensembles encoding their associations (Gelbard-Sagiv et al., 2008). The MTC is part of a network containing major memory-facilitators such as the hippocampus and sensory cortices like the visual cortex (Quiroga et al., 2008). Imagining original, fictitious scenarios or future events stimulate the same regions of the MTC, which filters information retrieved from the hippocampus and visual cortex in order to restructure them in novel ways (Heit et al., 1988; Hassabis et al., 2007). Both short-term and long-term memory retrieval is important in artistic conception, as an artist needs to be able to retrieve recent knowledge or sources of inspiration relevant to the task as well as of long-term memories that serve as foundational references (Kowatari et al., 2009). The specialization and spontaneous activation of neurons within the MTC (Kreiman et al., 2000) allow for the construction of new memories containing unique associations across semantic categories. The MTC and hippocampus play a vital role in the generation of new ideas, as these structures encode novel information, construct memories, and consolidate associations across other neural networks (Heit et al., 1988; Luo & Niki, 2003; Hassabis et al., 2007). This attunement towards novelty expedites the process of restructuring pre-existing ideas in order to form new associations (Rutishauser et al., 2006; Hassabis et al., 2007). Associative thinking, which is facilitated by the DMN, activates cell assemblies that are not activated or even inhibited during analytic thinking, which is a function of the CEN (Runco & Yoruk, 2014; Gabora, 2018). This is because defocused attention, which creates associative conditions, allows for the processing of encoded properties that are not directly relevant to the task at hand (Runco & Yoruk, 2014). The hippocampus is able to facilitate cognitive reorientation by providing context from memory between the inability to solve a problem and a fixation on conventional solutions, thus allowing for a shift in activation to novel associations (Luo & Niki, 2003).

The precuneus is involved in forming associations as well, as it facilitates intuitive mental imagery, as well as introspection and empathy (Carroll, 2020). This region of the DMN increases the pool of information available for idea formation as spontaneously recalled memories within the MTC can be combined with internally generated mental imagery facilitated by the precuneus. Artists and individuals with high divergent thinking scores, which indicate a strong ability to create original, variable solutions to open-ended problems (de Manzano et al., 2010), have more gray matter volume in the precuneus than non-artists and convergent thinkers (Takeuchi et al., 2010; Chamberlain et al., 2014). Fink et al. (2014) conducted functional magnetic resonance imaging (fMRI) while individuals performed cognitive flexibility tasks and found higher activation in the precuneus in highly creative people as compared to low creativity individuals. The precuneus also provides connectivity between association cortices like the TPJ and memory regions like the MTC (Ellamil et al., 2012). The TPJ is responsible for combining spontaneously generated information arising from the MTC and precuneus with external sensory information concerning a particular problem or goal (Decety & Lamm, 2007; Ellamil et al., 2012). This cortical area is involved in regulating visual awareness (Webb et al., 2016) and receives input from sensory and limbic areas that facilitates complex social reckoning as well as insightful problem-solving (Ellamil et al., 2012). Cellular activity within the TPJ filters the information passing through this area by relevance preliminarily, providing framework for top-down evaluation of information being internally generated in such an unconstrained manner (Wu et al., 2015). Information evaluated by the TPJ may be transmitted to the medial PFC for ultimate integration and resolution of ideas, as the medial PFC possesses executive circuitry (Ellamil et al., 2012).

The medial PFC possesses frontotemporal connections that give rise to artistic design and evaluation via memory retrieval (Chakravarty, 2012). Patients with medial PFC lesions are creatively impaired in terms of their ability to come up with original and appropriate responses to divergent thinking tests, indicating involvement of the medial PFC in creative insight (Shamay-Tsoory et al., 2011). Self-awareness is regulated by the medial PFC (Ebner et al., 2012), which aligns with this area's activation during aesthetic evaluation as circuits within the medial PFC integrate new memories of novel stimuli with emotional information. Using top-down control, medial prefrontal neurons retrieve long-term visual memory information from the ITC in the absence of bottom-up input (Tomita et al., 1999; Daffner et al., 2000). This promotes creativity by increasing potential visual memories that can be retrieved to form new associations. The medial PFC integrates novel memories with emotion regarding the conceptualized artwork that originates in the amygdaloid-hippocampal complex in the ATC (Miller, 2000; Koechlin et al., 2003). This integration occurs during the generation of creative insight as well as aesthetic evaluation. Insightful problem-solving is neurally correlated with a sudden burst of gamma activity in the temporal cortex and amygdala (Kounios et al., 2008; Ludmer et al., 2011) as an idea reaches consciousness via top-down selection facilitated by the medial PFC. Gamma oscillations occur at 20-50 Hz and are indicative of synchronized neural communication across and within networks during cognition and memory processing (Hughes, 2008). Gamma activity within the temporal cortex suggests working memory manipulation of novel memories. Gamma activation of the interconnected amygdala indicates long-term encoding of the “Aha!” solution, as the emotional charge of receiving spontaneous, rewarding ideas is memorable (Ludmer et al., 2011).

In order to form long-term goals that allow for the physical execution of an art project, ideas conceptualized within the medial PFC may be transmitted to the CEN via top-down selection. The ACC, which is involved in allocating attention over the various neural pathways within the PFC, connects the medial PFC to the CEN (Miller & Cohen, 2001; Crottaz-Herbette & Menon, 2006; Lavin et al., 2013). Both the medial PFC and the ACC are involved in internal emotional responses (Etkin et al., 2011), with the ACC selectively inhibiting or attending to information recalled from the temporal cortices by the medial PFC (Lane et al., 1997). Chakravarty (2012) proposed a neural circuit of art design and production that occurs via simultaneous activation of neurons within the medial PFC, temporal lobes, lateral PFC, occipital lobe, and SMA (Figure 5). Conceptual information integrated within the medial PFC is transmitted to the lateral PFC, which transmits input to the occipital lobe, SMA, and other areas of the motor cortex in order for the mental imagery to be tangibly expressed (Chakravarty, 2012). The transfer of information regarding artistic design from the medial PFC to the lateral PFC for production can be reversed as well, ensuring that the goal-directed behavior facilitated by the latter aligns with the conceptualization evoked by the former (Chakravarty, 2012). Connectivity between the medial PFC and lateral PFC is enhanced in professional artists as compared to non-artists, allowing for a balance to be formed between free-thinking and executive control (De Pisapia et al., 2016).

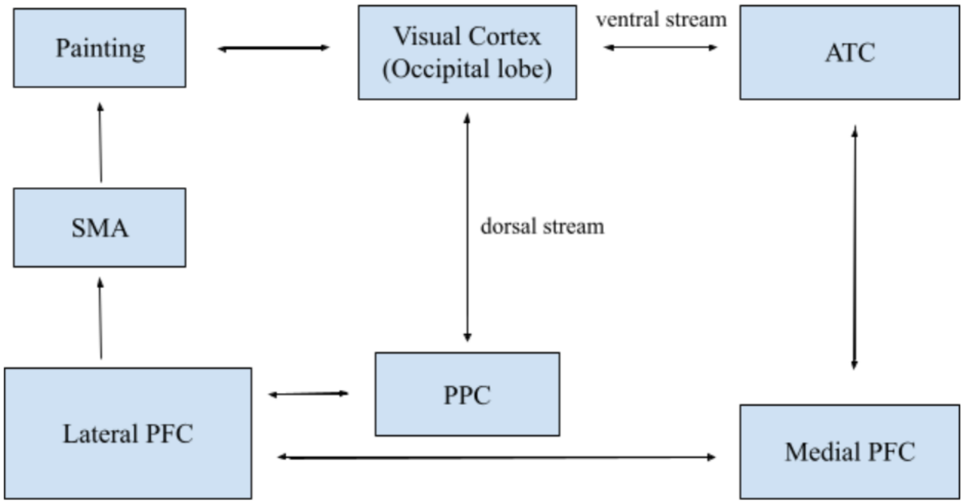

Figure 5. Possible neural circuit between structures of the CEN and DMN during visual art production, as proposed by Chakravarty (2012).

Central executive and default mode network coupling

It is evident that both the DMN and CEN are involved in idea generation, artistic evaluation, and expression. Due to their contrasting strategies of problem solving, these networks were initially thought to oppose and actively suppress each other (Fox et al., 2005). High creativity scores on chain free association tests, in which participants spontaneously verbalize a cascading list of associated words, are correlated with higher activation of the DMN and reduced activation of the CEN (Marron et al., 2018). Highly creative individuals have “more complex semantic memory structure and activate a wider range of associations across their semantic memory network”, which requires activation of the DMN and disengagement of the CEN (Kenett, 2018, p. 235). However, there is evidence of DMN and CEN co-activation during creative evaluation tasks (Kounios et al., 2008; Marron et al., 2018; Carroll, 2020). Though spontaneous mind-wandering often generates original chain free associations, mindful or deliberate mind-wandering enhances creative performance to a greater magnitude (Henriksen et al., 2020). During insightful problem-solving tasks, activation has been observed within regions of the DMN such as the precuneus, PCC, and TPJ, as well as regions of the CEN such as the ACC and dorsolateral PFC (Geake & Hansen, 2005; Kounios et al., 2008). Additionally, visual art production positively affects the DMN even though the CEN activates the premotor and visual areas necessary to execute drawing, painting, or printing. A fMRI study conducted by Bolwerk et al. (2014) found that adults older than sixty-two who consistently practiced drawing over a period of ten weeks with the goal of finding their own artistic style experienced strengthening of connectivity between the PCC and other regions of the DMN. The PCC is responsible for modulating attention between various regions in the DMN such as the medial PFC and MTC. An increase in functional connectivity between the PCC and medial PFC due to visual art production is positively correlated with an increase in psychological resilience, or the ability to resist stress (Bolwerk et al., 2014). This is likely due to the role of the medial PFC in regulating negative emotions and self-awareness (Wager et al., 2008; Jang et al., 2011), and emphasizes the therapeutic potential of visual art production relatively late in life. As visual art production increased connectivity within the DMN, this network is clearly involved in the process of finding one’s unique style of artistic expression, which requires introspective activation and visual imagery facilitated by the DMN.

These studies (e.g. Bolwerk et al., 2014; Marron et al., 2018; Henriksen et al., 2020) indicate that aspects of creativity are promoted by the integration of both deliberate and spontaneous processing styles. Some degree of executive focus facilitated by the CEN is beneficial while evaluating ideas in order to maintain focus. Conversely, unconstrained simulations formed by neurons within the DMN in conditions of low latent inhibition stimulate artistic expression. The balance between spontaneous and deliberate processes is demonstrated by comparing dreaming, mind-wandering, and creativity (Andrews-Hanna et al., 2018). Dreaming is completely spontaneous, with complete liberation of imagination as executive control ceases to guide behavior. Mind-wandering occurs when attention is directed internally and associations form spontaneously, but external stimuli are on the cusp of awareness and can easily interfere. Creativity involves both deliberate and spontaneous processes. Insight occurs freely, but executive focus on both internally and externally generated information is necessary to evaluate ideas and carry out the production of artwork.

As both networks are recruited during idea generation and evaluation, how does involvement of the DMN and CEN differ? The specific activation of the DMN during periods of low cognitive control allows for course, spontaneous semantic associations to form and reach consciousness as a burst of insight. This makes the DMN a facilitator of idea generation. The DMN may also regulate idea evaluation as it is involved in both external and internal emotional processing; this network contains connections to the amygdala, the center of emotional integration (Damasio et al., 2000; Kreiman et al., 2000; Satpute & Lindquist, 2019). DMN circuitry creates the formation of emotional intuition that may drive decision-making consciously or unconsciously (Finke, 1996). Thus, it makes sense that this network would have a significant impact on the evaluation of work. However, the DMN does not exert top-down control like the CEN does, which would allow for comparison of idea strength via specific selection and inhibition. Ellamil et al. (2012) used fMRI to examine activation within areas of the DMN and CEN while participants designed and drew a visual book cover design (2012). It was determined that CEN areas like the lateral PFC and dorsal ACC were most strongly activated only during idea evaluation, while DMN regions such as the MTC, medial PFC, precuneus, and TPJ, were significantly activate during both idea generation and evaluation.

While nodes of the DMN facilitate idea generation, both it and the CEN work together in the evaluation of creative ideas (Ellamil et al., 2012; Beaty et al., 2014). Creative thinking can be thought of as a dual process, involving both associative and executive attention that is mediated by coupling of DMN and CEN (Beaty et al., 2014). As the spontaneous and executive modes of processing that dynamically facilitate creative cognition are also involved in visual art production and aesthetic evaluation, large-scale coupling of the DMM and CEN promotes artistic skill. While the DMN facilitates spontaneous associative processes like mind-wandering, free chain association formation, and spontaneous retrieval from memory, the CEN facilitates the use of working memory and inhibiting of mundane ideas (De Pisapia et al., 2016; Marron et al., 2018).

The Salience Network and Dopaminergic Reward System

Interactions between the CEN and DMN regulate deliberate and spontaneous modes of processing, allowing for analysis of goal contingencies as well as the unconstrained formation of creative associations during the conceptualization process and/or symbolic interpretation of visual artwork (e.g., Ellamil et al., 2012). The third and final large-scale brain network that will be examined for its role in detecting salient, affective stimuli and regulating the independent or interactive engagement of the CEN and DMN is the SN. The SN monitors sensory input and autonomic feedback, identifies the salience and emotional valence of said input, integrates it with internal events and external demands, and switches activation to the most relevant large-scale network for resolution (Shi et al., 2018; Seeley, 2019). Cortical structures within the SN direct the 'spotlight' of attention towards visual stimuli that are novel or that stand out strongly while facilitating habituation of repetitive stimuli via sensory gating. The processing of salient stimuli is not primarily facilitated via filtration within SN structures (Menon & Uddin, 2010). Instead, this network evokes a cascade of cognitive control signals that dynamically activate subsequent pathways for the perception of a stimulus. This cascade ultimately leads to the switching of activation between the CEN and the DMN (Sridharan et al., 2008; Menon & Uddin, 2010).

The SN is comprised of cortical and subcortical limbic structures such as the anterior insula (AI), ACC, ventral striatum, and amygdala (Menon, 2015; Seeley, 2019). The ACC is functionally shared between the SN and CEN and provides circuitry for the transmission of information from the DMN's medial PFC to the CEN's lateral PFC (Sridharan et al., 2008). The ACC responds to salient information when it applies to conflict resolution or tasks requiring cognitive control, activating CEN neurons in order to evoke premotor planning within the SMA (Menon, 2015). The AI is associated with introspective detection of social and emotional information and is an integration center for the limbic system (Augustine, 1996; Menon, 2015). The AI coordinates dynamic switches between large-scale networks regardless of task paradigm and stimulus modality (Sridharan et al., 2008; Menon & Uddin, 2010), and provides autonomic feedback from the heart, lungs, and skin to the SN in order to activate the CEN or DMN, depending on which will functionally allow for the resolution of homeostatic needs. The ventral striatum facilitates the recall and processing of long-term memory with strong emotional associations by engaging with the amygdala and hippocampus (Alcaro et al., 2007; Flaherty, 2005). This area promotes novelty seeking and reward attainment as it contains the nucleus accumbens, which provides input to the basal ganglia for the execution of reward-seeking behaviors (Nicola, 2007). The ventral striatum thus serves as a limbic-motor interface, as it is involved in planning and executing movement related to goal attainment (Báez-Mendoza & Schultz, 2013). A cortico-striatal-thalamic loop circuit allows for the transfer of information between the SN and premotor areas such as the SMA (Peters et al., 2016). Finally, the amygdala is heavily implicated in emotional processing, particularly in response to fearful or threatening stimuli (Baxter & Croxson, 2012). Altogether, this group of structures make up the SN, which therefore functions to process salient and emotional cues arising both externally and internally.

The SN drives visual art processes independently of modulating CEN and DMN activation. Emotion serves as a significant driving force for artistic creativity, as it underlies unconscious thought, inspiration, and personality traits (Feist, 1998; Oriol et al., 2016). Neural circuits within the SN are able to process and differentiate emotion valences as they detect visual saliency. Stoica et al. (2017) defines visual saliency as the property of a scene to draw the attention of different people to the same objects within it. Visual salience is accomplished by emphasizing innate perceptual strategies within the visual system that differentiate global and local cues by color, line, texture, et cetera. Though the beholder's share elicits individual differences in emotional response to artwork, there is a universal consistency in what colors and patterns attract peoples' gaze (Stoica et al., 2017). Though variation in artistic expertise across individuals affects rankings of beauty within paintings, it does not impact evaluation of the emotional content of artwork (van Paasschen et al., 2015). Paintings that contain a certain organizational composition that is perceived as "visually right" are rated highly regardless of one's experience with the arts (Locher et al., 1999, p. 262). These findings suggest that the visual system and SN evolved to detect certain artistic principles over others, likely due to their biological relevance in premodern societies (Dissanayake, 2000). These salient principles evoke hardwired emotional responses; bright colors and smooth lines generally evoke positive feelings while dark colors and chaotic lines elicit negative feelings (Yanulevskaya et al., 2012). The essential dimensions of all emotions can be categorized into hedonic value and/or arousal value (Gu et al., 2018). From the point of homeostasis, all emotions contain value and valence that allow for biological adaptation to one's environment and approach/avoidance towards cues that may not be directly homeostatically relevant but are significant in terms of long-term fitness or goal attainment (Damasio and Carvalho, 2013). The ACC has been discussed for its role in interpreting the emotional content of artwork as part of the CEN (Etkin et al., 2011; Braem et al., 2017), but is not the only SN structure involved in affective processing. The AI facilitates detection of and empathy for painful facial expressions depicted in visual artwork (Ardizzi et al., 2021). The amygdala is activated by highly arousing or significant imagery (Ewbank et al., 2009), triggering strong emotional reactions that may activate the sympathetic nervous system. A full range of emotional valences may be evoked by the visual arts, including anger, confusion, and disgust as well as pleasure (Silvia, 2009). In fact, experiencing negative emotions may lead to greater artistic inspiration and production (Akinola & Mendes, 2008). The SN's role in processing complex emotional responses triggered by salient input facilitates an intrinsic motivation to be artistically expressive and responsive (Oriol et al., 2016; Gu et al., 2018).

The SN is highly interconnected with the DRS, which is activated by reward cues and forms hedonic associations that underly behavioral responses geared towards reward or goal attainment (Arias-Carrión et al., 2010). The DRS is regarded as the pleasure system of the brain and as a neural system overlaps with areas of the SN such as the insula and ventral striatum (Arias-Carrión et al., 2010; de Manzano et al., 2010). The release of the neurotransmitter dopamine (DA) modifies and consolidates neural activity across various regions of the brain in order to form cue-related associations that motivate an organism towards attaining rewards such as food, copulation, or viewing a beautiful piece of artwork (Arias-Carrión et al., 2010; de Manzano et al., 2010). Reward-seeking behavior and anticipation of a reward activate dopaminergic neurons within the PFC and ventral striatum, which serve to motivate the continuation of such behavior (Arias-Carrión et al., 2010). Reward anticipation is fueled by reinforcement of associations between cues and rewards that are learned over time. Because rewards exist across a spectrum of necessity- making artwork, for example, is not a survival requirement like gathering food is- the modulation of hedonic value within a single neural system allows for relative differentiation of reward functions. Correlations between DRS activity and creativity, art production, and aesthetic evaluation are well documented (e.g., Takeuchi et al., 2010; Lacey et al., 2011; Kaimal et al., 2017; de Manzano et al., 2017). Creative insight and the perception of aesthetically pleasing artwork are often accompanied by a rush of pleasure; this is due to the release of DA within the nucleus accumbens, which leads to activation of cortical regions such as the PFC and ITC in order to drive these rewarding processes (Oh et al., 2020). Additionally, DA may affect the visual saliency of artwork as it regulates cone sensitivity to color (Shuwairi et al., 2002).

The DRS is far more developed within humans than in other primates (Sousa et al., 2017), with increased DA production allowing for complex regulation of goal attainment. Being able to recognize and sustain motivation for long-term or abstract goals via cognitive control was a significant factor in the dominance of the modern human species. Dopaminergic innervation of the disproportionately large PFC, as well as other areas associated with emotional and social processing, likely evolved as humans lived in increasingly large and organized social groups (Yamaguchi et al., 2015; Raghanti et al., 2018). DA signaling has been implicated in social cooperation, empathy, facial recognition, aggression, and vocal communication within social hierarchies. By increasing sensitivity to social cues, increases in DA within humans promoted survival and reproduction (Raghanti et al., 2018). Dysregulation of DA levels within the nervous system may lead to various psychopathological diagnoses, including attention deficit hyperactivity disorder (ADHD), ASD, schizophrenia, bipolar disorder, addiction, and more (Alcaro et al., 2007; Durstewitz et al., 2008; Yamaguchi et al., 2015; Kyaga, 2018). While these psychiatric disorders may not seem advantageous to fitness, they are often symptomized by amplifications or reductions in potentially beneficial cognitive functions such as creativity, impulsivity, and the construction of associative memory (Yamaguchi et al., 2015). The relationship between creativity and psychopathology will be discussed later on.

The majority of dopaminergic neurons are found within the ventral tegmental area (VTA) and substantia nigra, both of which are connected to the SN (Menon, 2015; Caminera

& Cascella, 2020). Cells within these areas facilitate signal integrations that coordinate reward-seeking behavior across the brain, an impressive feat considering that dopaminergic neurons make up less than 1% of the brain's total neuronal population (Arias-Carrión & Pŏppel, 2007; Decot et al., 2017). This is aided by the fact that a major dopaminergic pathway in the brain originates in the VTA, giving it extensive connectivity to various brain regions (Arias-Carrión et al., 2010). The mesocorticolimbic system emerges from the VTA, with the mesolimbic pathway projecting into the striatum and the mesocortical pathway connecting to the PFC (Alcaro et al., 2007; Takeuchi et al., 2010). The mesolimbic and mesocortical pathways work together in order to regulate emotion-based behavior in relation to reward attainment or punishment avoidance. The combined connectivity of the mesocorticolimbic system to the striatum and PFC allow for complex affective and analytic reward processing. The mesolimbic pathway projects into the ventral striatum, and contains neurons that detect errors in reward prediction, correcting one's behavioral and emotional response to a cue (McCutcheon et al., 2019). This error detection is facilitated by striatal connections to long-term memory storage areas and is applied in the understanding of other's goals and emotions as well as to one's own (Badgaiyan, 2010; Báez-Mendoza & Schultz, 2013). Stimulation of mesolimbic DA neurons activates nodes of the SN (Decot et al., 2017), increasing connectivity within this network in properly attribute hedonic value to environmental cues (McCutcheon et al., 2019).

As it projects into the lateral PFC, the mesocortical system is involved in optimizing higher-order processes such as cognitive flexibility, executive focus, processing of abstract symbolism, and decision-making in relation to reward attainment (Gonzalez-Burgos et al., 2005; Pariyadath et al., 2016). The PFC is sensitive to the effects of DA, as it contains a high frequency of specialized receptors that cause persistent action potential firing (Gonzalez-Burgos et al., 2005; Cools & D'Esposito, 2011; Zaidel, 2016). DA significantly impacts how much information is retained in working memory during higher-order cognitive tasks being facilitated by the PFC, as well as the reward value of goal attainment. Neurons within the mesocortical pathway interact with the mesolimbic system in order to regulate hedonic impulses via the integration of cognitive and affective information (Arias-Carrión et al., 2010). While the mesolimbic pathway facilitates reward learning and cognitive flexibility, the mesocortical pathway promotes effort learning and executive attentional focus (Cools & D'Esposito, 2011; Hauser et al., 2017). The anatomical and functional segregation of these pathways allows for multiple potential decisions to be processed simultaneously in the evaluation of cost/benefit analysis.

Activation of the DRS and DA binding within structures of the SN, CEN, and DMN are positively correlated with network connectivity, intrinsic motivation, flow states, and the perception of beautiful imagery (Lacey et al., 2011; de Manzano et al., 2012; Ulrich et al., 2014; Shafiei et al., 2019), thus playing a major role in creative insight, art production, and aesthetic evaluation. DA decreases latent inhibition (Flaherty, 2005), which facilitates creativity (Carson et al., 2003). Individual differences in the genetically determined structure of the mesolimbic DA system are correlated with expression of personality traits (Alcaro et al., 2007) that may be associated with increased creativity, such as impulsivity and novelty-seeking (Feist, 1998). The release of DA and subsequent decrease in latent inhibition within the PFC and striatum facilitated by the mesocorticolimbic system creates a balance between cognitive stability and flexibility, or convergent and divergent thinking (Cools & D'Esposito, 2011). Interactions between variations of the gene COMT, which promotes DA degradation within the PFC, and the gene DAT, which facilitates DA reuptake in the striatum, have been linked to factors of divergent thinking such as originality, fluency, and flexibility (Zabelina et al., 2016). Thus, individual variation in reward perception may cause differences in creativity.

Divergent thinking has been strongly correlated with the function of dopaminergic D2 receptors. Polymorphisms of the D2 receptor gene DRD2 TAQ IA have been associated with individual differences in divergent thinking performance, regardless of general intelligence (Reuter et al., 2006). This gene is involved in the regulation of regional D2 receptor density and binding potential. Low D2 binding potential within the thalamus, which regulates the mesocortical system, is often a significant marker for creativity (de Manzano et al., 2010). This reduced binding potential decreases thalamic sensory gating, which allows more subcortical signals to pass through this region and excite cortical regions of the brain responsible for the attentional integration of novel, creative ideas (de Manzano et al., 2010). Takeuchi et al. (2010) found a positive correlation between regional gray matter volume within the substantia nigra and striatum and divergent thinking scores. It is speculated that an increase in striatal gray matter may be correlated with an increase in DA binding, which decreases latent inhibition and thus allows for spontaneous creative insight. Additionally, the availability of D2 receptors within the striatum has been positively linked to one's ability to enter flow states, which describes a state of high focus, enjoyment, and low self-awareness that accompanies one in the performance of a rewarding, challenging task such as art production (de Manzano et al., 2012).

Unprompted conceptualization or idea generation facilitated by the DMN is associated with reward signals regulated by the DRS (Oh et al., 2020). The striatum, amygdala, hippocampus, and medial PFC are all activated following insightful realizations of novel semantic relationships (Kizilirmak et al., 2019). Oh et al. (2020) determined that there is likely a positive relationship between problems solved via insight and reward value. Additionally, feelings of pleasure may increase sudden solution realization as well as insight accuracy (Subramaniam et al., 2009). A rush of pleasure following creative insight may reinforce intrinsic motivation to tangibly express ideas, or to spend more time mind-wandering.

The DRS is also implicated in aesthetic evaluation of visual artwork. The medial PFC, which has been investigated for its role in self-awareness and creative idea generation as part of the DMN, is implicated in a dopaminergic reward circuit containing the ventral striatum and amygdala during aesthetic evaluation of visual art (Lacey et al., 2011). This circuit is activated selectively by visual art; non-art imagery does not cause a response. This neural discrimination is representative of evolutionary advantages for being able to have aesthetic experiences evoked by visual art. Additionally, the medial PFC is exclusively activated by artwork that is particularly beautiful or aesthetically pleasing (Chatterjee & Vartanian, 2014). It is thought that the perception of beautiful stimuli activates neurons within the medial PFC, which transmit signals to the ATC, where visual features that have been associated with beauty or pleasure are processed by the hippocampo-amydaloid complex (Chakravarty, 2012). The SN and DRS are then activated in order to compute an emotional and hedonic response. While beauty is certainly influential in aesthetic experiences of pleasure, it is not a necessary component of emotionally moving and aesthetically engaging visual artwork (Silvia, 2009; Pearce et al., 2016). Rankings of beauty are subjective (Pearce et al., 2016), depending on perceptual preferences that vary across individuals by culture and biology (Yue et al., 2007; Chatterjee, 2011). Viewing emotionally moving artwork can trigger changes in heart rate, pupil size, et cetera, regardless of the emotional valence (Chatterjee, 2013). These autonomic reflexes are detected by the AI and thus transmitted throughout the SN and potentially the CEN and/or DMN. Because the DRS mediates responses to aversive stimuli as well as pleasing stimuli (Smith et al., 2009), visual artwork that evokes disgust or fear likely activates the DRS, though perhaps not as much as pleasing art does.

The medial PFC-ventral striatum-amygdala reward circuit is activated by visual art production as well as aesthetic evaluation. Kaimal et al. (2017) used fNIRS to examine brain activity in humans during participation in artistic expressions such as doodling, coloring, and free drawing. All three of these conditions stimulated this circuit regardless of experience level, age, and gender. Doodling, which was defined as unstructured drawing of personal style within a certain frame, created the most reward perception and pleasure (Kaimal et al., 2017). This is likely because it evoked more intrinsic self-expression guided by memories recalled by the medial PFC, and the individual preferences in style led to increased reward perception within the striatum. While creative practices positively evoke a response from the DRS, highly creative individuals have a genetic vulnerability to mental and behavioral disorders.

Dopaminergic and salience-based correlation between creativity and psychopathology

There is a wide overlap in personality and cognitive traits associated with creativity and psychopathological disorders such as schizophrenia, bipolar disorder, ADHD, and major depressive disorder (Fink et al., 2014; Kyaga, 2018; Piffer, 2018). Open-mindedness, impulsivity, novelty-seeking, divergent thinking, diffuse attention, reduced latent inhibition, and neural hyperconnectivity are often symptomatic of highly functional creative people as well as those with mild to severe psychiatric impairment. These traits are often products of dopaminergic regulation within the brain (Alcaro et al., 2007) and may thus be genetically inherited (Kyaga, 2018; Piffer, 2018). This supports the presence of a biological correlation between creativity and psychopathology. There commonly exists an idea that talented artists must suffer from psychopathological disorders to order to hone their craft, with supporting references to some of most famous artists throughout history such as Edvard Munch, Vincent van Gogh, and Yayoi Kusama, who all experienced varying severities of psychosis as well as depression and mania (Wolfe, 2001; Suma et al., 2018; Skryabin et al., 2020). While these case studies illuminate the existence of talented artists with psychopathological disorders, there are mixed findings on whether highly creative individuals or artists have a greater prevalence of mental disorders than the general population (cf., Ludwig, 1992; Pavitra et al., 2007; Kyaga et al., 2013; Baas et al., 2016; Taylor, 2017). There is likely an inverted-U shaped effect of psychopathology on creativity, with the positive creative effects outweighing the negative cognitive effects only in mild to intermediate forms of psychopathological impairment (Carson, 2018; Piffer, 2018). This is supported by schizotypal individuals, who are predisposed to psychosis without showing actual schizophrenic psychopathology, having higher divergent thinking scores than both non-impaired individuals and schizophrenics (Folley & Park, 2005). Kyaga et al. (2013) found that first-degree relatives of patients with schizophrenia and bipolar disorder were overrepresented in creative professions, as they likely have genetic predispositions towards divergent thinking, diffuse attention, and reduced latent inhibition while lacking diagnostic, deleterious symptoms of these disorders.

Fink et al. (2014), who determined higher activation of the precuneus in highly creative people as compared to low creative individuals, found that schizotypal individuals show similar functional brain activity patterns during the formation of creative ideas. This suggests that creativity and psychosis share similar cognitive processes that recruit the DMN. There are many neural similarities between artistic creativity and psychopathologies in the DRS in particular. Reduced D2 receptor binding potential in the thalamus is a marker of schizophrenia as well as creativity (de Manzano et al., 2010). Decreased thalamic sensory gating thresholds caused by low D2 binding potential may excessively overwhelm cortical areas, leading to cognitive disorganization and psychotic thoughts and behavior, which are symptomatic of schizophrenia. Additionally, polymorphisms of the DRD2 TAQ IA gene, which have been correlated with creativity (Reuter et al., 2006), have also been associated with schizophrenia and bipolar disorder (Golimbet et al., 2003; Wang et al., 2014). Finally, DA promotes novelty-seeking, which has been correlated with addiction and other psychiatric disorders when unbalanced (Costa et al., 2014). DA antagonists are commonly used to treat psychotic disorders and are reported to suppress creative drive as reducing DA activity in the brain impairs neural processes that have been implicated in both psychopathology and creativity (Flaherty, 2005; Ashok et al., 2017).

Various mood disorders, such as major depressive disorder and bipolar disorder, can be attributed in part to dysregulation of mesolimbic DA transmission (Alcaro et al., 2007). While depression inhibits creative drive, artistic people have higher rates of depression than average (Flaherty, 2005; Nestler 2015). It is speculated that the rate of art production increases during the energized recovery periods in between bouts of depression rather than in the midst of depression (Jamison, 1989). The manic episodes often experienced by patients with bipolar disorder also allow for intense periods of creation; increased activity and focus along with decreased prioritization of sleeping and eating allow for continuous visual art production. Mania is associated with unbalanced D2 receptor activity within the striatum and can thus be thought of as an extreme and unbalanced flow state, which is also correlated with striatal D2 receptor availability (de Manzano et al., 2012; Ashok et al., 2017).

SN impairment has been associated with psychopathological vulnerability as well; delusions and hallucinations associated with schizophrenia may occur due to the misattribution of salience to internally generated stimuli (Menon, 2015). Schizophrenics show reduced volume in the AI and ACC (Menon, 2015); neurons within these areas are activated during network switching between the CEN and DMN (Sridharan et al., 2008). Manoliu et al. (2014) found that interactions within and across the CEN and DMN are compromised by schizophrenia due to decreased AI activity, leading to impaired self-regulation and task performance. Strengthening functional connectivity between networks may help to protect against neurocognitive vulnerability towards psychopathology (Carson, 2018). Thus, the SN's function in mediating activation of the DMN and CEN is crucial in effectively balancing aspects of creativity such as low latent inhibition, divergent thinking, and associative hyperconnectivity, preventing cognitive disorganization and affective impairment.

Dynamic interactions between large-scale networks

Switching between dominant activation of large-scale brain networks promotes flexible attention, which is positively correlated with creativity (Gabora, 2010). Zabelina (2018) proposed a model of creativity and attention that presents creative achievement as a function of divergent thinking, high cognitive control, and "leaky" or nonfiltered attention. Creative artistry is thus a product of switching attention between different networks initiated by salient stimuli; individual creativity is positively associated with the efficacy of attention reallocation (Takeuchi et al., 2010). If salient stimuli require externally directed cognition, the SN will activate the CEN, whereas internally directed cognitive tasks cause the SN to activate the DMN (Menon & Uddin, 2010). Interactions between strategies of cognition or styles of attention has been emphasized for their role in facilitating complex artistic and creative processes via switching between the CEN and DMN (e.g., Ellamil et al., 2012; Zabelina, 2018). The SN is able to mediate engagement of the CEN and DMN simultaneously, preventing the functions of one network from dominating the other. While an integrated balance of divergent thinking, high cognitive control, and leaky attention facilitate creativity, any one of these processes can lead to various negative effects if left unchecked. Without high levels of cognitive control emerging from the CEN, for example, leaky attention may lead to psychopathological issues like schizophrenia (Zabelina, 2018). However, highly filtered states of attention prevent unconventional associations from forming within the DMN (e.g., Bowden et al., 2005; Fink et al., 2009). As it allocates attention towards the opposing functions of the CEN and DMN, the SN is a critical system for facilitating the complex creative processes, including conceptualization, visual art production, and aesthetic evaluation. Regional gray matter volume within structures of the SN is positively correlated with creativity, as such artistic tasks often require both externally and internally directed attention (Shi et al., 2018).

The CEN and SN interact closely and directly, even being considered "fraternal twins" by Seeley as they anatomically overlap within the ACC (2019, p. 9879). The SN detects the relevance of semantic, episodic, perceptual, and affective information that is transmitted into in working memory for the CEN to manipulate (Chrysikou, 2018). During cognitively demanding tasks, the SN activates the CEN via the lateral PFC, PPC, and ACC (Menon & Uddin, 2010). The AI has a powerful causal influence on ACC outflow in particular (Sridharan et al., 2008), as it is also involved in the regulation of attention switching and emotional valence (Miller & Cohen, 2001; Etkin et al., 2011). Both the AI and ACC contain von Economo neurons that are relatively large with simple dendritic projections into other network structures, suggesting functional specialization towards the rapid transmission of control redirection (Allman et al., 2012). This type of neuron is only present within humans and other great apes, providing a cellular basis for complex cognitive processes including social intuition and empathy. The ACC and parts of the insula respond to salience regardless of its goal-related value (Bartra et al., 2013), which is sequentially determined by structures in the CEN via top-down signaling. Sridharan et al. (2008) determined via fMRI that activation of the AI and ACC predict disengagement of the DMN during higher-order tasks that require executive focus, indicating that the SN and CEN may work together to negatively regulate the DMN (Chen et al., 2014). These findings were determined by using Granger causal analysis, which determines the extent to which signal changes in one area of the brain predict signal changes in other regions (Menon & Uddin, 2010).

The SN is able to regulate DMN activation as well as DMN disengagement. Coupling between the AI and PCC was present during idea generation for an alternate uses test, demonstrating simultaneous activation of the SN and DMN (Beaty et al., 2015). A lack of DMN suppression or deactivation originating from the SN allows for spontaneous generation of intrinsic stimuli that are later transmitted through the SN and CEN for "abstraction, comparison, and response selection" (Nikolaidis & Barbey, 2018, p. 392). While highly controlled cognitive task and unconstrained association-making respectively require selective activation of the CEN or DMN, visual art processes require a dynamic balance between deliberate analysis and spontaneous associations (Ellamil et al., 2012; Beaty et al., 2014). Idea evaluation, for example, activates CEN and DMN simultaneously (Ellamil et al., 2012). Beaty et al. (2015) used fMRI to examine brain activity during creative tasks requiring both cognitive control and spontaneous insight in order to determine how the SN, CEN, and DMN interact. Towards the beginning of divergent thinking tasks, the SN and DMN coupled within insular regions, indicating internal attention. At later stages, the SN and CEN coupled in order to facilitate top-down cognition. Additionally, connectivity between CEN and DMN structures increased during creative tasks; the lateral PFC and PCC/precuneus were directly connected and activated while thinking creatively (Beaty et al., 2015). Creative insight, visual art production and aesthetic evaluation all require dynamic balances of activation in networks specialized towards novel association formation, cognitive control, and low latent inhibition that are triggered and regulated based on artistic content, environmental context, and individual variation in neurocognition (e.g., Chakravarty, 2012; Cela-Conde et al., 2013; Chrysikou et al., 2014; Zabelina, 2018). Possible neural circuitry between the SN, CEN, and DMN during artistic processes is shown Figure 6.

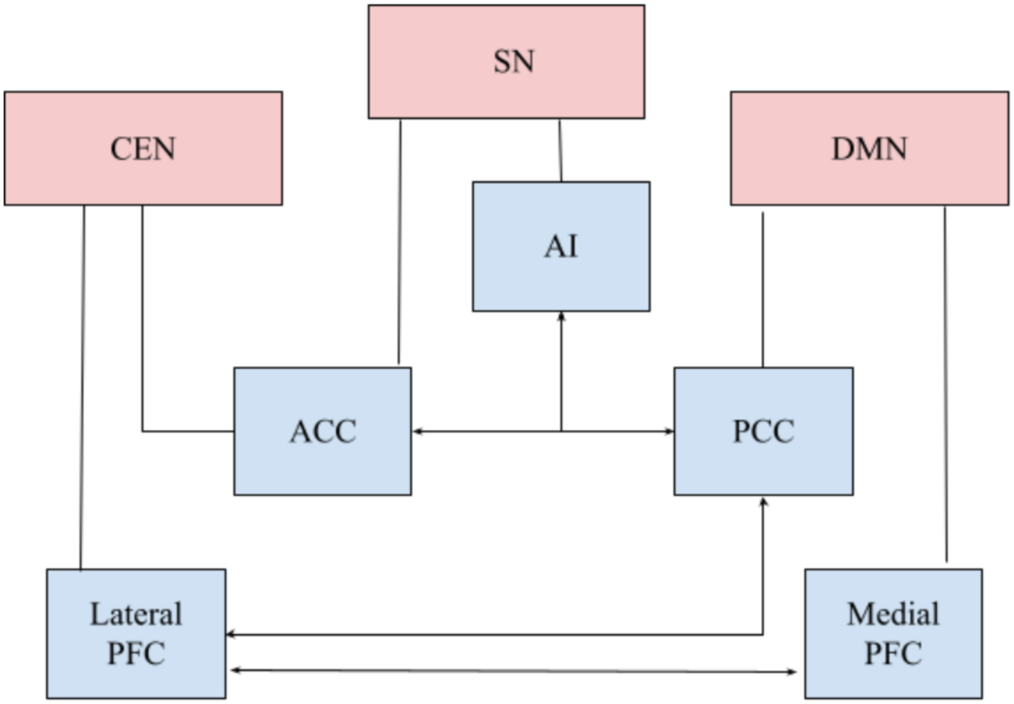

Figure 6. Possible network interactions during visual art engagement.

The DRS is also involved in network dynamics, as DA concentration is positively correlated with large-scale network connectivity, particularly between the SN and other networks such as the CEN and DMN (Cole et al., 2013; Shafiei et al., 2019). Functional between-network connectivity forms via temporal synchronization of neuronal signaling, which is regulated by DA. This principle aligns with Hebb's rule, which predicts increases in synaptic strength following temporal synchronization in activation (Hebb, 1949). The release of DA throughout the DRS and SN influences how network nodes switch allegiance or facilitate interactions between networks (Shafiei et al., 2019). DA is thought to dynamically regulate a balance between cognitive flexibility and stabilization (Cools & D'Esposito, 2011) via the mesocorticolimbic system. Additionally, DA circuits throughout areas of the SN, DMN, and CEN facilitate pleasure responses following visual art production, aesthetic evaluation, and creative insight (Lacey et al., 2011; Kaimal et al., 2017; Oh et al., 2020). Feelings of pleasure enhance creativity (Davis, 2009), creating a sort of feedback loop between art engagement and positive mood. This correlation has implications for the therapeutic value of visual art engagement.

Making visual art has been found to reduce short-term stress levels, strengthen long-term psychological resistance to stress, increase positive feelings, and improve one's sense of self-efficacy regardless of age, gender, race and previous artistic experience (Bolwerk et al., 2014; Kaimal & Ray, 2017; Kaimal et al., 2017). Belkofer et al. (2014) determined that drawing leads to enhanced alpha activity, which is associated with relaxation and self-regulation, within frontoparietal regions of the brain. Creating visual artwork may be task-oriented approach to therapy for people experiencing hyper-vigilant states of arousal that are often present in ASD, generalized anxiety disorder and post-traumatic stress disorder (PTSD) (Belkofer et al., 2014; Jones et al., 2019; Lopes, 2021). Similarly, Kruk et al. (2014) found that clay sculpting may induce a meditative state and decrease stress. Intrusive, traumatic memories are often encoded and recalled in vivid imagery rather than in words (Clark & Mackay, 2015). Being able to express these images through drawing, painting, or sculpting may offer catharsis to those struggling with PTSD (Jones et al., 2019). Additionally, doodling may improve cognitive performance by increasing memory retention (Andrade, 2010), which could have useful applications in school systems or for people with ADHD (Lopes, 2021). Finally, the activation of DRS pathways following visual art production may serve as a replacement for other addictive behaviors that trigger the same neural circuits (Feen-Calllgan, 2013; Kaimal et al., 2017). SN function is also implicated in art therapy;

repetitively making and evaluating visual artwork increases mindfulness, a state of enhanced awareness and acceptance that is associated with increased functional connectivity between the SN, DMN, and CEN (Doll et al., 2015; Fogo, 2017). While the CEN directs focus onto the present experience, DMN facilitates spontaneous visualizations, and the SN allows for conscious awareness of mind-wandering by connecting the two networks (Hasenkamp & Barsalou, 2012). The strength of functional connectivity between the CEN, DMN, SN, and DRS regulates multi-faceted engagement with the visual arts as well as psychological wellbeing. The role of the SN and DRS in processing arousal and hedonic value and dynamically regulating large-scale network activation is crucial in creative and artistic processes.

Conclusion

This review explored the evolutionary and neural mechanisms of visual art conceptualization or creative idea generation, production, and aesthetic evaluation. An emphasis on network interactions and functions illuminated the role of the CEN, DMN, SN, and DRS in visual art engagement. Specifically, creative and artistic processes appear to require coupling between these large-scale brain systems that may not ordinarily exist or that is not activated by other processes that are strictly analytic or associative (e.g., Beaty et al., 2018). The large-scale functions of the CEN and DMN are activated by the SN (Sridharan et al., 2008; Ellamil et al., 2012; Beaty et al., 2015), allowing for analytic, executive, and deliberate processing facilitated by the CEN to be coupled with associative, spontaneous, and unconstrained processing emerging from the DMN. Together, the SN, CEN, and DMN facilitate creative, artistic processes that require varying processing and attentional styles for optimal performance (Ellamil et al., 2012; Beaty et al., 2015; Zabelina, 2018). The DRS consolidates activity across neural circuits within these networks, evoking feelings of pleasure following engagement with the visual arts that builds intrinsic motivation for future artistic endeavors (e.g., Lacey et al., 2011; Kaimal et al., 2017; Oh et al., 2020). As Ellamil et al. described creative evaluation, visual artistic processes "may thus be an extended form of analytic processing that combines processes that do not ordinarily act in tandem in order to produce optimal thinking conditions for creativity" (2012, p. 1791).

The complex spatial and functional capacities of the networks discussed in this review allowed for the conscious prioritization of visual arts within premodern cultures, a trend that is universally present across modern societies (Ramachandran & Hirstein, 1999; Morriss-Kay, 2010). As *Homo sapiens* evolved, pressures on group cohesion led to the development of neural circuits that elicited symbolic expressions such as language and imaginative simulations that promoted social intuition (Zaidel, 2020). Additionally, the ability to generate and evaluate ideas allowed for the realization of novel and useful solutions for environmental challenges (Wiggins et al., 2015). Neural pathways that developed for symbolic practices were later exapted towards the production and perception of visual artwork, which was created during religious rituals to promote group identity and the cultural imposition of meaning on one's environment (Dissanayake, 2000). Similarly, the neurocognitive ability to aesthetically evaluate objects or scenes for signals of quality or danger was applied to visual artwork, evoking emotional responses that are shaped by hardwired, biological cues as well as iconographical and iconological interpretations that vary across individuals (Stebbing, 2004; Kandel, 2012). The ability to think creatively and gain spontaneous insight further enhanced artistic novelty and the distinction of group identity.

Creative, artistic processes are not specialized towards one anatomical region, as they rely on a variety of dynamic and possibly oppositional functions arising from large-scale networks specialized towards cognitive control, spontaneous association formation, visual saliency and emotional valence processing, and reward sensitivity. Coming up with ideas for art projects, creating such artwork via painting, sculpting, or other mediums, and aesthetically evaluating visual art made by oneself or by others are all complex tasks that require both externally and internally directed attention and connectivity to higher-order cortices as well as limbic, motor, and visual system areas. Neural networks are functionally diverse and dynamic, and interactions between the CEN, DMN, and SN may promote conditions of flexible attention that promote the visual arts (Beaty et al., 2018; Nikolaidis & Barbey, 2018).

Sensory input processed and manipulated within large-scale networks emerges from visual memory and processing structures within the visual system. The visual system constructs three-dimensional visual fields and thus processes sensory cues that inform and guide artistic processes (e.g., Grossberg, 2008; Kandel, 2012). The ability to maintain focus on abstract, evaluative processes is a product of cognitive control and top-down processing mechanisms emerging from neurons within the lateral PFC, PPC, and ACC, which form the goal-directed CEN (Miller & Cohen, 2001; Beaty et al., 2015). Spontaneous association formation and the integration of self-referential and social information facilitated by the DMN's medial PFC, MTC, precuneus, and PCC in the absence of externally directed attention allows for creative ideas and concepts to form (Raichle et al., 2001; Bowden et al., 2005). While functions of the CEN and DMN seem to be contradictory and simultaneous activation of these two networks may impair performance on intellectual tasks (Fox et al., 2005), artistic tasks follow a dual processing model that implicate both cognitive stability and flexibility (e.g., Beaty et al., 2018; Zabelina, 2018).

The recognition of salient or pleasing ideas and artwork emerges from the SN and DRS, which together include the AI, ventral striatum, amygdala and mesocorticolimbic system (Arias-Carrión et al., 2010; Seeley et al., 2019). Both systems facilitate intrinsic motivation, with the SN dynamically engaging the CEN and DMN depending on what the task at hand requires (Sridharan et al., 2008; Menon & Uddin, 2010). For example, idea generation selectively engages the DMN while evaluation recruits both the DMN and CEN (Ellamil et al., 2012; Beaty et al., 2015; De Pisapia et al., 2016). Though most studies on interactions between these networks have been in relation to creative idea generation, there is reason to believe that visual art production and aesthetic evaluation also recruit functional connectivity between these networks (e.g., Lacey et al., 2011; Chakravarty, 2012; Kaimal et al., 2017). Future research on network activation patterns during visual art production and aesthetic evaluation could help to elucidate how the functional contributions of each network specifically affects different stages of artistic processes.

While the neural mechanisms that facilitate visual perception of and cognitive engagement with the arts via creative conceptualization, execution, and evaluation are biologically hardwired across humans, individual variations in creativity and artistic inclination can be predicted by differences in functional connectivity these networks, as well as DA sensitivity and visual perceptual strategies (e.g., Kozbelt, 2001; Reuter et al., 2006; Bolwerk et al., 2014; Schlegel et al., 2015; Zabelina et al., 2016; Beaty et al., 2018;

Nikolaidis & Barbey, 2018; Yeshurun et al., 2021). Additionally, neurocognitive variation across individuals caused by ASD, FTD, and/or a wide range of other psychopathological disorders including schizophrenia and bipolar disorder significantly influences artistic tendencies, content, and rate of production (e.g., Mendez, 2004; Drake & Winner, 2009; Carson, 2018; Piffer, 2018). Conversely, creative and artistic processes have the ability to strengthen neurocognitive functioning and resilience to psychological stress (Bolwerk et al., 2014; Kaimal et al., 2017; Jones et al., 2019). Though not discussed in this review, hemispheric lateralization also plays a significant role in creative and artistic processes (e.g., Coney & Bruce, 2004; Kowatari et al., 2009; Mihov et al., 2010; Gonen-Yaacovi et al., 2013; Belkofer et al., 2014).

The importance of the visual arts to human culture cannot be understated. Creative forms of expression such as painting, drawing, and sculpting are unique to our species, and offer a sense of meaning and connections with others that satisfies a universal inclination towards novel and emotionally rich stimulation. As Dissanayake writes, “art has become a repository for what remains of human spiritual longing and emotional expression in a nonreligious world founded on technological and rational solutions to human problems” (2000, p. 170). Humans are able to engage with the visual arts because of advanced and complicated development of specialized large-scale brain networks within modern *Homo sapiens*, which were co-opted for artistic processes as a conscious way to promote connection with others through expressing emotionally moving imagery reflective of one’s internal states or external circumstances (e.g., Zaidel, 2013; Agnati et al., 2013). As a function of remarkably capable and diverse networks within the brain, the visual arts have become an intrinsic part of the human experience.

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