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# 3

# Neuroscience, Biology, and Brain Evolution in Visual Art

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Self-knowledge, insight into all phases of life and mind, springs from artistic imagination. That is the cognitive value of the arts.

(Langer 1962: 82)

Symbolic cognition is one of the hallmarks of the human mind. Visual artists are able to create something new on canvas, something that did not exist previously and does not actually exist in reality, even when, at times, it closely resembles reality, precisely because of this abstract and symbolic cognition. What the creation expresses is what is on the artist's mind, which includes conscious and unconscious experiences, political and cultural events, beliefs, fears, desires, emotions, and much more. The list is endless. Above all, the composition communicates a message from artist to viewer. Art is a communicative system able to relay ideas in ways not afforded in language alone.

The neuroscientific basis of art is a puzzle if only we consider that some symbolic behavior has been observed in animals as well, including non-human primates (Addessi *et al.* 2008; de Waal and Tyack 2003). Admittedly, not full-blown pervasive symbolic behavior as is observed in humans, but symbolic nevertheless. And, yet, animals do not produce art (one exception perhaps is the bowerbird (Diamond 1982; Miller 2000; Zaidel 2009, 2010). The fact that they do not would suggest that a certain threshold of symbolism capacity, abstraction, and referential cognition must be reached before art can be produced (to say nothing of other neuroanatomical and neurochemical underpinnings). Whatever that threshold level might be, and regardless of when and how in evolutionary times it was reached, it could have given rise to additional human communicative systems as well, namely language, body language, hand gestures, and facial expressions. The precursors must have been in place for millions of years, since non-human primates have their own vocalization language, body language, hand gestures, and facial expressions (Premack 2007; Remedios *et al.* 2009). Other critical

brain capacities, then, ones that are unique to humans, must play significant roles in art production.

We often think of human language as the prime example of symbolic cognition. While the neurological basis of language has been extensively studied in the past 150 years, and quite a bit is now known and understood regarding how it is organized in the brain, attempts to zero in on the neuroanatomical underpinning of art are greatly hampered by absence of clear definitions of the components of pictorial art (or any art). Neuroscientists and neuropsychologists need reducible (defined) components to be able to link them to neural regions and pathways. Currently, except for spatial organization required in pictures, a function specialized in the right parietal lobe, there is no simple way of achieving such definitions. On the other hand, the whole of pictorial production may indeed be more significant than its parts, and general components may be sufficient. Skills, talent, and creativity are good examples of such components.

Several intriguing and relevant issues to the neuroscience of art are discussed in this chapter. (1) Brain regions and visual sensory considerations: The appearance of art stems from both sensory properties, namely the eyes themselves, and central properties, namely brain regions specialized in processing spatial cognition, color knowledge, and aesthetics. (2) *Homo sapiens* evolution: When did the symbolic cognition threshold reach a level that triggered abundant art production by *Homo sapiens* and what else happened simultaneously by way of cognitive changes? (3) Biology and sexual selection strategies: The display feature of pictorial art might be explained in biological motivation terms, ones that involve neural motivational systems in the brain particularly associated with mate selection strategies (Miller 2000, 2001; Zahavi 1978; Zaidel 2010).

## 1. Peripheral sensory influences

Vision is influenced by neurological events, starting with the eye itself and ending in the vision processing regions of the brain. In this regard, several scenarios with potential effects on the appearance of art can be drawn. The first concerns the clarity of the artist's sensory vision arising from physical structures within the eye, such as the crystalline lens and retina. Distortions and fuzziness in the composition can be caused by the shape and elasticity of the lens, or they can be caused by abnormal or diseased arrangements of the photoreceptors in the retina, and other eye-related causes.

Consider visual processes and the use of colors in paintings. The first stage in seeing colors resides in retinal photoreceptors known as cones, which are situated in the back of the eyeball, and are in fact specialized neurons (Hubel 1995). The fovea is located in the retina and through its anatomical and physiological makeup facilitates focused vision. The cones enable us to see colors with chemical reactions triggered by the lightwaves entering the eye and hitting the fovea. The contex, via several subcortical sub

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synaptic stations. In the occipital lobes reside the primary visual areas where neuronal computations are performed on the signals arriving from the synaptic stations and resulting in conscious perception of colors. But suppose, for example, there is abnormality in the cones in the first place, as in colorblindness (color deficiency). In such cases colors are not perceived normally. More of one cone receptor type than another or a complete absence of a receptor skews the lightwave information reaching the brain, particularly the vision processing regions in the occipital lobes. The condition is caused by genetic transmission of a mutation on the maternal X chromosome, typically affecting males. In colorblindness cases, some colors end up being seen as shades of gray. A colorblind artist can be the best painter in the world but when it comes to colors, the eye's physiological condition impacts the choice of colors (Lanthony 2001). Several such artists have been identified (for review see Zaidel 2005). With noncolorblind artists, it is not known why artists apply their own unique coloring techniques (Van Gogh and Matisse, for example) or the nature, organization, and dynamics of the cones across non-artists. Whatever colors are applied by individual artists, colorblind or not, they reflect, in part, the physiological and anatomical status of the cones.

Other eye-related issues affect pictorial representation. An eye disease such as retinal degeneration where the neurons in the retina degenerate (e.g., Degas), or a cataract in the crystalline lens (e.g., Monet, Cassatt), or normal aging of the eye (e.g., Rembrandt, Titian) (Jackson and Owsley, 2003; Spear, 1993) would all prevent lightwaves from impacting the cones in a normal fashion. Fuzzy vision, abnormal perception of colors, and inaccurate perception of details can result from such eye diseases. Moreover, the cones being specialized neurons are actually an extension of the brain and are affected by neurotransmitters present in brain tissue. For example, dopamine, a major neurotransmitter in the brain, has many receptors on the cones themselves and too much or too little of this neurotransmitter impacts the way some colors, particularly blue, are seen and applied pictorially (Djamgoz *et al.* 1997; Masson *et al.* 1993).

# 2. Brain and aesthetic sensations

The organization of our psychological capacities in the brain is traditionally inferred from consequences of damage to the brain. To my knowledge, there have been no reports of loss of aesthetic responses following any type of brain damage. Alterations in visual aesthetics following brain damage have been documented in a single published case, again to the best of my knowledge. A few cases of dementia where there was moderate brain atrophy have been described for musical preference alterations (reviewed in Zaidel 2005). A man suffering from temporal lobe epilepsy and who underwent left anterior temporal lobectomy reported changes in his music, literature, and painting preferences (Sellal *et al.* 2003). Before surgery he preferred rock music, science fiction literature, and abstract paintings; after surgery his taste shifted to polyphonic singing, novels, and realistic paintings. This neurological case is unusual. In the absence of a critical mass of evidence for aesthetic alterations, there is too little to go on to reach conclusions. Importantly, a study of aesthetic preference in Alzheimer's patients found no statistically significant difference in preference between the patients and the normal controls, despite presence of major cognitive deficits in the patients (Halpern *et al.* 2008). Collectively, the large-scale absence of aesthetic preference alterations following brain damage, of any etiology or localization, as well as absence of reports for loss of aesthetic reactions, suggests a diffuse functional representation of aesthetics processing in the brain (see discussion, Zaidel 2005: 159–60).

Across historical times aesthetic reactions appear remarkably stable. Consider modern-day preference for ancient or cross-cultural art. Art created in one side of the world by cultures speaking languages and adhering to customs no one can understand on the other side of the world can nevertheless trigger aesthetic reactions in that side. Context is a critical clue to understanding the nature of art, and still without understanding the context of a distant culture we react aesthetically to its art. This suggests a context-free, culture-free neuronal foundation for aesthetic reactions, perhaps one rooted in ancestral biological motivational systems linked to reproduction (discussed in subsequent paragraphs of this chapter). It should be mentioned, however, that we do not have evidence of aesthetic reactions, per se, in animals; aesthetic assessment may be uniquely human.

A few neuroimaging studies investigated preference for paintings. The results implicate brain activity in several regions and little agreement among the studies (reviewed in Nadal *et al.* 2008). Some of these studies have discussed involvement of the motivational system known as the "reward pathway." The system consists of the forebrain bundle, lateral hypothalamus and its "pleasure center," and the excitatory neurotransmitter dopamine. However, recent animal work demands reconsideration of the role the "reward pathway" and dopamine play in motivational behavior (Burgdorf and Panksepp 2006; Panksepp 2005). The limbic system, dorsolateral prefrontal cortex, and other subcortical regions as well as the endorphins, and the inhibitory neurotransmitter GABA are also involved in experiential pleasure and positive affect. Thus, it is not unreasonable to expect aesthetics and its pleasure-related reactions to have brain origins other than the "reward pathway." Moreover, not all aesthetic experiences are linked to pleasure in a straightforward way: For example, horror and tragedy in art do not lead to clear-cut pleasure. In the context of aesthetics, then, reward and pleasure are not necessarily the same thing.

# 3. Brain damage effects in artists

Visual artists with brain damage can shed light on the relationship between art and brain regions. This is accomplished through examination of the post-damage works and comparing to pre-damage output. The issues concern any alterations, loss of talent, skill, or creativity. Approximately forty cases with unilateral damage or with diffuse damage have been described thus far in the neurological literature, and a review of the

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majority of these cases indicates that on the whole artists go on producing art despite the damage and, importantly, independently of its laterality or localization (Zaidel 2005). So this suggests that artistic talent, skill, and creativity, to say nothing of ideas, concepts, and symbolic cognition, are generally diffusely represented in the brain and no single "center," region, or pathway controls art-related cognition and production.

Furthermore, no specific technique or style alterations are associated with localization of the damage, or its etiology. Artists accustomed to using the abstract art *genre* (style) adhere to it following damage, and the same is true of the realistic style pre- and post-damage. This implies that the neurological foundations of *genre* are diffusely represented, and through redundancy of functional representation survive regional damage (Zaidel 2010). Some brain-damaged artists develop techniques to compensate for loss of perceptual and cognitive specialization. However, these techniques are subtle and difficult to group into coherent categories.

Specific art-related alterations can nevertheless be explained in terms of loss of perceptual and cognitive specialization controlled by particular brain regions, although similar deficits are observed in non-artists suffering from damage in the same brain regions. One example is loss of accurate depictions of spatial relations, particularly as they apply to three-dimensional space (3-D). These deficits are observed following damage in the right parietal lobe (De Renzi 1982). Another example is the phenomenon of hemi-neglect. The condition typically occurs following damage in the right hemisphere, in the parietal lobe, and manifests in hemi-neglect of the left half of space where the left half of the canvas would be largely unfilled. The neglect symptoms often have short time duration, lasting approximately six weeks or so in the majority of cases. Regardless, the essence of pictorial art does not lie in its spatial layout alone, certainly not in two-dimensional (2-D) depictions of 3-D space, so functions specialized in the right parietal lobe cannot be regarded as the core essence of pictorial art. Instead, the cognitive functions specialized in both cerebral hemispheres should be regarded as being involved in the whole artistic process, and only future research could decipher the balance of individual hemispheric contributions.

## 4. Biological motivations in art production

The energy put into an artistic creation, its purpose and function, the continued experimentation and innovations by artists, and the impact on the observer, have all been interpreted against a background of biological motivation. Specifically, it has been proposed that art, whether visual or not, serves as means for the display of talent, skill, and the artist's genetic quality (Miller 2000, 2001; Zahavi 1978). According to this view, the need to exhibit art is rooted in mate selection display strategies for the purpose of procreation and promulgation of their species. Such courtship displays, the most famous of which is the stunning display of the peacock's tail, have driven sexual selection in evolutionary dynamics (Cronin 1992; Darwin 1871). Just as the peacock fans out his tail to reveal perfections and imperfections stemming from genetic fitness,

disease, parasites, and strength, so do artists reveal quite a bit about their cognitive prowess, which includes skill, talent, and creativity, by exhibiting their compositions. Art is produced principally in order to display to others.

This biological motivational background of art is consistent with its communicative essence. There is a mutually receptive interaction between the producer and the viewer emanating from an earlier biological level than the symbolic and abstract. Courtship signals in animals are meant to attract attention and maintain interest long enough for procreation; the displays are varied, as they are spectacular. They characteristically involve body parts and motor control that historically evolved to advertise fitness in the most optimal ways. The male bird of paradise not only displays fitness, health, and genetic quality in his elaborate feathers and acrobatics, but also in the various shades of color reflected from his feathers. All of this is meant to expose quality level for the critical assessment by potential female mates aiming for healthy offspring (Gould and Gould 1989). The position adopted in this chapter is that the foregoing is a reasonable way to explain how the motivation behind exhibition and display in animals drives the motivation for display of human art, and attract our attention to the message.

# 5. *Homo sapiens* and evolutionary cognitive and neurological changes

Extensive symbolic and abstract cognition is associated with Homo sapiens. The fossil record points to Africa where Homo sapiens first emerged around 150,000-200,000 years ago (Mellars 2006b; Relethford 2008). There is archaeological and genetic DNA evidence that anatomically modern humans migrated away from Africa to other parts of the world at least a couple of times. The first migration, around 100,000 years ago, did not spread extensively throughout Europe and Asia. However, traces of symbolic cognition associated with this group have been uncovered in sites located both in South Africa and in Israel, including symbolic burials, red ochre pigments of different shades, which had to be transported into cave shelters over long distances, as well as ornamentations (Hovers et al. 2003; Jacobs et al. 2008; Mellars 2006b). The second migration out of Africa around 60,000-65,000 years ago did lead to a wider dispersion throughout Europe and Asia (Behar et al. 2008; Mellars, 2006b). This migration brought with it from Africa more sophisticated tool technology than the first migration. In the intervening years since the first migration, cognitive and neurological changes are assumed to have proceeded in Africa based on archaeological evidence of finer, more sophisticated tools. Locations in South Africa, in particular, have revealed refined hand tools and ornamentations at more advanced levels than other regions in this continent (Henshilwood and Marean 2003; McBrearty and Stringer 2007), and it is the South Africa ancestors that are believed to have formed the second migration (Mellars 2006a). In the absence of substantially large archaeological and fossil data from the period of the intervening years, it is only speculation as to what led to the cognitive

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and neurological changes. One explanation rests on substantial evidence for serious climatic events in Africa, particularly droughts lasting for over 100,000 years, leading to isolation of human groups who nevertheless survived by harvesting new sources of food and living along seacoasts where seafood was abundant (Jacobs *et al.* 2008; deMenocal 2011). Both the nutrients available in such food and the methods to harvest it could have contributed greatly to the increased symbolic and advanced technology.

However, archaeological evidence for full-blown art production is lacking from these sites in Africa and other places in the world. Developed art does not appear on the modern human scene until around 35,000–45,000 years ago, and when it does appear, it is in Western Europe. And therein lies the mystery: the time gap between the appearance of *Homo sapiens* and the emergence of abundant practice of art. In addition, given that anatomically modern humans had spread to so many regions by then, why was art produced abundantly only in Western Europe? What was the role of humans' closest relatives, the Neanderthals, who were already present in Western Europe for more than 300,000 years when *Homo sapiens* arrived, in the big art explosion (Balter 2009)? Presently, these remain outstanding questions. Clearly, cognitive and neuroan-atomical changes occurred gradually over biological time, altering and modifying in the context of natural selection and adaptation to the environment (Zaidel 2010).

As mentioned in the initial paragraphs of this chapter, cognitive and neurological thresholds must be reached in order to produce art. This level may not be unique to art; it could include many forms of communication as well. In the debate concerning the role and emergence of art in human societies not all agree with the biological reproductive link arguments (described in section 4). Another point of view links art principally to a simultaneous development of sophisticated grammatical language, with the latter leading the way. This view implies that the hallmark of symbolic cognition in humans was triggered first and foremost by language development. According to the language-symbol argument, the primary brain alteration was linguistic cognition with art being secondary or a byproduct. One proposal for the genetic trigger for language development is the FOXP2 gene (Enard et al. 2002). However, doubts have been raised about any unique role of FOXP2 in human language since this gene is found in animals as well (Fisher and Scharff 2009). In sum, a major change in the brain of the anatomically modern humans, associated with the period of the initial abundant art in Western Europe, is hypothesized by some evolutionary scholars (Klein and Edgar 2002).

However, not everyone agrees with this view of a sudden and major brain change (Holden 2004), including the present author. The debate is ongoing. The dynamics of biological changes are slow and gradual over time; they are subject to evolutionary adaptive changes and natural selection forces (Hernandez *et al.* 2011). The anatomical and physiological precursors of humans' sophisticated grammatical language with its combinatorial syntax had to have been in place for millions of years before 45,000 years ago (McBrearty and Stringer 2007; Remedios *et al.* 2009; Zaidel 2005, 2009). Besides, there is no convincing evidence that the earliest *Homo sapiens* lacked language; they

may very well have had elaborate grammatical language. However, what could have happened around 45,000 years ago in Western Europe is some critical change in the behavior of the anatomically modern *Homo sapiens* that facilitated consistent production of art, a practice that has increased since then and gone unabated to this day. The critical behavior is likely to have a genetic and neuroanatomical basis. For example, it has recently been suggested that there was an increase in group size, intra-group cooperation, spike in altruism leading to group cohesion, and as a result long-term survival of talented, skilled individuals, were all pivotal changes (Bowles 2009; Mace 2009; Powell *et al.* 2009). These possibilities are highly plausible and could serve as new insights into speculations and debates on the origins of art practice.

## References

- Addessi, E., Mancini, A., Crescimbene, L., Padoa-Schioppa, C., and Visalberghi, E. (2008). Preference transitivity and symbolic representation in capuchin monkeys (cebus apella). *PLoS ONE*, 3: e2414.
- Balter, M. (2009). New work may complicate history of Neanderthals and H. sapiens. *Science*, 326: 224–5.
- Behar, D. M., Villems, R., Soodyall, H., Blue-Smith, J., Pereira, L., Metspalu, E., Scozzari, R., Makkan, H., et al. (2008). The dawn of human matrilineal diversity. American Journal of Human Genetics, 82: 1130–40.
- Bowles, S. (2009). Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? *Science*, 324: 1293–8.
- Burgdorf, J. and Panksepp, J. (2006). The neurobiology of positive emotions. *Neuroscience and Biobehavioral Review*, 30: 173–87.
- Cronin, H. (1992). The Ant and the Peacock. Cambridge: Cambridge University Press.
- Darwin, C. (1871). The Descent of Man, and Selection in Relation to Sex. London: John Murray.
- deMenocal, P. B. (2011). Climate and human evolution. Science, 331: 540-2.
- De Renzi, E. (1982). Disorders of Space Exploration and Cognition. New York: Wiley.
- De Waal, F. B. M. and Tyack, P. L. (eds.) (2003). Animal Social Complexity: Intelligence, Culture, and Individualized Societies. Cambridge, MA: Harvard University Press.
- Diamond, J. (1982). Rediscovery of the yellow-fronted gardener bowerbird. Science, 216: 431-4.
- Djamgoz, M. B. A., Hankins, M. W., Hirano, J., and Archer, S. N. (1997). Neurobiology of retinal dopamine in relation to degenerative states of the tissue. *Vision Research*, 37 (Special Issue: Vision and Neurodegenerative Diseases): 3509–29.
- Enard, W., Przeworski, M., Fisher, S. E., Lai, C. S. L., Wiebe, V., Kitano, T., Monaco, A. P., and Paabo, S. (2002). Molecular evolution of FOXP2, a gene involved in speech and language. *Nature*, 418: 869–72.
- Fisher, S. E. and Scharff, C. (2009). FOXP2 as a molecular window into speech and language. *Trends in Genetics*, 25: 166–77.
- Gould, J. L. and Gould, C. G. (1989). Sexual Selection. New York: Scientific American Library.
- Halpern, A. R., Ly, J., Elkin-Frankston, S., and O'connor, M. G. (2008). "I know what i like": Stability of aesthetic preference in Alzheimer's patients. *Brain and Cognition*, 66: 65–72.

- 52 THE PSYCHOLOGY OF THE AESTHETIC
- Henshilwood, C. S. and Marean, C. W. (2003). The origin of modern human behavior. *Current Anthropology*, 44: 627–51.
- Hernandez, R. D., Kelley, J. L., Elyashiv, E., Melton, S. C., Auton, A., Mcvean, G., Project, G., Sella, G., and Przeworski, M. (2011). Classic selective sweeps were rare in recent human evolution. *Science*, 331: 920–4.
- Holden, C. (2004). The origin of speech. Science, 303: 1316-19.
- Hovers, E., Ilani, S., Bar-Yosef, O., and Vandermeersch, B. (2003). An early case of color symbolism: Ochre use by modern humans in Qafzeh Cave. *Current Anthropology*, 44: 491–522.
- Hubel, D. H. (1995). Eye, Brain, and Vision. New York: W. H. Freeman.
- Jackson, G. R. and Owsley, C. (2003). Visual dysfunction, neurodegenerative diseases, and aging. *Neurological Clinic*, 21/3: 709–28.
- Jacobs, Z., Roberts, R. G., Galbraith, R. F., Deacon, H. J., Grun, R., Mackay, A., Mitchell, P., Vogelsang, R., et al. (2008). Ages for the Middle Stone Age of Southern Africa: Implications for human behavior and dispersal. Science, 322: 733–5.
- Klein, R. G. and Edgar, B. (2002). The Dawn of Human Culture. New York: Nevraumont.
- Langer, S. K. (1962). Philosophical Sketches. Baltimore: Johns Hopkins University Press.
- Lanthony, P. (2001). Daltonism in painting. Color Research & Application, 26: S12-S16.
- Mace, R. (2009). On becoming modern. Science, 324: 1280-1.
- Masson, G., Mestre, D., and Blin, O. (1993). Dopaminergic modulation of visual sensitivity in man. *Fundamentals of Clinical Pharmacology*, 7: 449–63.
- McBrearty, S. and Stringer, C. (2007). The coast in colour. Nature, 449: 793-4.
- Mellars, P. (2006a). Going East: New genetic and archaeological perspectives on the modern human colonization of Eurasia. *Science*, 313: 796–800.
- (2006b). Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. *Proceedings of the National Academy of Sciences USA*, 103: 9381–6.
- Miller, G. F. (2000). *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature*. New York: Doubleday.
- (2001). Aesthetic fitness: How sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria. *Bulletin of Psychology and the Arts*, 2: 20–5.
- Nadal, M., Munar, E., Capó, M. A., Rosselló, J., and Cela-Conde, C. J. (2008). Towards a framework for the study of the neural correlates of aesthetic preference. *Spatial Vision*, 21: 379–96.
- Panksepp, J. (2005). Affective consciousness: Core emotional feelings in animals and humans. Consciousness and Cognition, 14: 30–80.
- Powell, A., Shennan, S., and Thomas, M. G. (2009). Late Pleistocene demography and the appearance of modern human behavior. *Science*, 324: 1298–1301.
- Premack, D. (2007). Human and animal cognition: Continuity and discontinuity. Proceedings of the National Academy of Sciences USA, 104: 13861–7.
- Relethford, J. H. (2008). Genetic evidence and the modern human origins debate. *Heredity*, 100: 555–63.
- Remedios, R., Logothetis, N. K., and Kayser, C. (2009). Monkey drumming reveals common networks for perceiving vocal and nonvocal communication sounds. *Proceedings of the National Academy of Sciences USA*, 106: 18010–15.

Sellal, F., Andriantseheno, M., Vercueil, L., Hirsch, E., Kahane, P., and Pellat, J. (2003). Dramatic changes in artistic preference after left temporal lobectomy. *Epilepsy and Behavior*, 4: 449–51.

Spear, P. D. (1993). Neural bases of visual deficits during aging. *Vision Research*, 33: 2589–2609. Zahavi, A. (1978). Decorative patterns and the evolution of art. *New Scientist*, 19: 182–4.

Zanavi, A. (1976). Deconarie patients and the evolution of art. 1969 Octamist, 19, 162 4.

- Zaidel, D. W. (2005). *Neuropsychology of Art: Neurological, Cognitive, and Evolutionary Perspectives.* New York and Hove, UK: Psychology Press.
- (2009). Brain and art: Neuro-clues from intersection of disciplines. In M. Skov and O. Vartanian (eds.), *Neuroaesthetics*. Amityville, NY: Baywood, pp. 153–70.
- (2010). Art and brain: Insights from neuropsychology, biology and evolution. *Journal of Anatomy*, 216: 177–83.