

Research Article

Assimilating Neuroimaging with the Archaeology of Early Mark-Making: A Critical Assessment

Derek Hodgson¹

1. Independent researcher

The earliest known engravings display a concern for repetitive lines and motifs that date from over 500,000 years ago onwards, which has led to a variety of suggestions as to their significance. Of the three main competing hypotheses as to their import, one—based on neuroimaging evidence—posits that they are fully symbolic, whereas the second proposes a proto-aesthetic explanation based on the way the visual cortex processes information, while the third—material engagement theory—is based on kinesthetic affordances. The aim of this paper is to assess the merits of each approach by presenting recent evidence from neuroscience, neuro-archaeology and material engagement theory in order to attain a more unified evaluation of the significance of the engravings. In order to facilitate that aim, a critical assessment of the advantages and limitations of employing various neuroimaging techniques is undertaken. Recent research from neuroaesthetics is also presented to show how it can provide useful insights into early mark-making, especially in the context of proto-aesthetics.

Introduction

Zeki^[1] considers visual art as a type of experiment that artists engage in, albeit unconsciously, that simulates the way the brain functions. In other words, as visual art is created by dint of the brain it must, therefore, obey its rules. Zeki's approach provides a platform for considering the probable significance of the first marks that appear in the archaeological record, what might be called 'pre-art'. Such marks have been the subject of much debate, especially thanks to research that derives from recent neuroscience, perceptual psychology and material engagement theory. In what follows, we will

be assessing the contribution of those disciplines to understanding how and why early humans first began to make repetitive marks and basic geometric patterns.

The controversy over the status of the earliest engravings has given rise to a number of empirical studies that have endeavored to provide insights into their ‘meaning’^{[2][3]}. In that regard, a series of neuroscientific investigations to assess their import was carried out where subjects viewed marks similar to those made by fossil humans, which came to the conclusion that they are probably symbolic or representational^{[4][5][6][7]}; hereby referred to as the ‘symbolic model’. This was mainly based on the finding that the visual area active when subjects view marks similar to early engravings is largely confined to the higher visual regions where objects are perceived as such, including where the Visual Word Form Area (VWFA) is located (though some mid to lower regions, especially LOC [Lateral Occipital Cortex], were also found to be active). That conclusion, however, contradicted earlier theoretical studies indicating that such marks may be related to how the early visual cortex (namely areas V1, V2, V4 and LOC) processes perceptual information based on a proto-aesthetic sense as defined by the Neurovisual Resonance Theory^{[8][9][10][11]}, henceforth NRT. Contrary to the findings of the neuroimaging studies, research on visual perception by Tylén et al.^[2] provided support for NRT and, to a certain extent, so does material engagement theory^[12].

In a critical response to the symbolic model, Hodgson^{[13][14][15]} provided copious evidence from extensive neuroscientific research demonstrating that the early visual cortex (EVC) encodes and processes visual information by first extracting simple features important for beginning to discriminate edges, corners, vertices; a process that begins in V1 and is assembled into successively complex configurations as visual information ascends the visual hierarchy. That evidence, however, also emphasized the role of feedback from higher visual areas to EVC, which is recruited according to task demands, such as discriminating fine detail and confirming the authenticity of incoming perceptual information. Thus, there is a dynamic interaction between bottom-up and top-down contingencies. In short, Hodgson’s theoretical position, not only takes account of the entire visual stream within the visual cortex, but also how the lower and higher levels interact, and not just V1 as mistakenly stated by supporters of the symbolic model.

Limits of fMRI and Early Engravings

An important point of diversion with the symbolic model is that a large and burgeoning corpus of neuroscientific investigations employing fMRI (Functional Magnetic Resonance Imagery), EEG (Electroencephalography) and MEG (magnetoencephalography) found that the earliest areas of the visual cortex play a critical role in processing basic line configurations (see below for details of this research). The symbolic model, however, failed to find any response from V1 up to LOC. Yet one of those studies^[6] actually found activity at lower levels when experts viewed simulated early patterns, namely the occipital pole where V1 is located^{[16][17]} but that finding was deemed inconsequential. This, despite the fact a number of fMRI studies have found activity occurring at earlier levels, i.e., V1 to LOC, when subjects viewed similar configurations to those of early engravings^{[18][19][20][21][22][23][24][25][26][27][28]}, yet the symbolic model continues to claim otherwise. That may be because of certain limitations pertaining to fMRI as a technique relating to the fact that, although the procedure has good spatial resolution, it suffers from low temporal resolution^[23], as epitomized in the following statement:

Although fMRI can inform us about which cortical areas are involved in contour integration, it does not allow tapping into the temporal aspects of the grouping processes, and the dynamic feedforward and feedback processes.^[23] (p.10)

Due to that limitation, neuroscientists recommend that fMRI should be used in conjunction with EEG, as well as MEG (the two latter which have excellent temporal resolution but less spatial accuracy) in order to attain a fuller picture of brain activity^[29]. This is especially the case when attempting to record activity in early visual areas where feedforward onset is particularly rapid, usually around 60 milliseconds, whereas activity in the higher visual areas occurs later at 80-100 milliseconds^[28]. fMRI, because it relies on blood oxygenation levels, can be regarded as a correlate or proxy of neural activity rather than an immediate measure of such activity because the blood flow alterations on which it depends occur seconds after any changes to neural activity— considerably slower than the millisecond timescale of EEG and MEG measurements^{[30][31]}. As a result, a growing number of neuroscientists recommend employing either both or all three procedures because they recruit different physiological fundamentals^{[32][31]}. By employing those techniques in conjunction, researchers would therefore be better placed to make inferences about the neural foundations of cognitive activity.

Where EEG has been employed to determine brain responses to simple patterns, the early visual cortex was indeed found to be active. In fact, studies have already been carried out combining fMRI and EEG protocols^[23]. In the EEG analysis, it was established that local to global (LG) processing activates the early visual cortex around 70 ms, whereas integrated global (GO) processing only activates the higher visual cortex at around 200 ms to 270 ms. Importantly, no difference was registered differentiating LG and GO when utilizing fMRI. Note LG refers to local feature extraction such as grouping, collinearity, line discrimination, and figure/ground segmentation, and GO to generalized holistic processing. These results confirm an intimate link exists between high-level shape/object areas and low-level retinotopic regions V1 and V2 in terms of the integration of local elements into a global shape. This suggest that the symbolic model should have included an EEG protocol to determine the timing of events in the visual cortex, as fMRI may well have not picked up the early activity in the lower visual cortex (as mentioned above, however, one of the fMRI studies carried out by the symbolic proponents, namely Salagnon et al.^[6], did find activity in the visual pole where V1 is located).

There is one other factor that could have biased the neuroscientific findings, namely fMRI needs to be designed specifically to detect activity in V1 and EVC. For example, an fMRI analysis was carried out by Ress and Heeger^[33] that was set up to detect such activity, which duly found changes in V1 where subjects viewed repetitive patterns when attempting to discern figure from ground.

Suppression of V1 and EVC

A further problem with the symbolic model is that it does not take into account the possibility that, when a coherent shape is successfully processed from incoming information regarding line data issuing from early visual cortex, activity in lower areas is suppressed. In other words, the realization of a coherent shape configuration can actually ‘turn off’ or attenuate activity in EVC, including V1. Thus, when subjects in the Mellet and Salagon studies viewed the simulated engraved patterns that were seen as coherent shapes or patterns, the early visual cortical areas may have undergone such suppression. This is in line with recent theoretical findings borne out by neuroscience of ‘predictive encoding’^{[34][35][36]}. In effect, when incoming visual information has gone through the initial lower-order sifting stage in EVC, it is then passed to the higher feedforward areas in the occipitotemporal to inferotemporal cortex where the larger shape Gestalt is realized, which ultimately leads to the attenuation of the lower-order areas. This is because, for example, V1 has greater sensitivity to local image features, including grouping of line segments^[37], whereas higher object sensitive areas are

capable of grouping local image features into global shapes, thus the need for lower areas to signal their presence is diminished^{[38][39][35]}. In contrast to the feedforward stream, that procedure involves feedback projections from higher to lower areas that dampen activity in EVC. As Murray et al. state^[38] (p.15169):

Our interpretation of these results is that when line segments are grouped with the background or combined into a pattern (i.e., have reduced saliency), V1 activity is reduced, as in the current study.

That reduction seems to be because of the need to simplify the description of a visual image and preserve neural resources by increasing efficiency^[40]. Note the above studies were carried out employing fMRI, which is the same procedure utilized in the symbolic model. That finding further underscores the need to utilize other brain imaging techniques, such as EEG and MEG, that capture temporal criteria.

Based on the above analysis, I would suggest that, because the ancient patterns employed in the symbolic model are well structured Gestalt configurations, their fMRI data simply shows that the higher-order visual areas had already suppressed activity in EVC, and this is why V1 and associated lower regions are not registered in the symbolic fMRI protocols.

A further criticism that can be levelled at the symbolic model is that they assume that NRT uniquely prioritizes V1, when that theory emphasizes the dynamic relation between V1, EVC, and higher visual areas involving the above mentioned feedforward and feedback channels. That process involves contour integration at all levels of the visual cortex from earliest to later areas that reflects the statistical properties of the natural environment^[41]. The main difference between the lower and higher levels seems to be that the former deals with smaller portions of information whereas the latter is concerned with more global features. Yet the later areas are as dependent on the lower areas both for the feedforward 'construction' of features as much as in the feedback scrutiny of details based on the principles of Gestalt organization^[42]. In addition, feedback from higher visual areas may account for the sensitivity of V1 to particular contours, particularly when this involves closed shapes^[18]. In general terms, that scenario fits with forward prediction models of how the visual cortex functions, where mismatches between higher and lower levels are continuously updated depending on how difficult or complex the incoming visual data is^[23].

The finding of the symbolic model that the left fusiform gyrus undergoes greater activity than the right hemisphere may ultimately be an artefact in the sense that the activation may arise from the fact that ordered lines stimulate that area because they automatically trigger the underlying heuristics the visual system appropriates for parsing objects. In that sense, VWFA has been found to be sensitive to novel abstract line configurations that are “word-like” in that they do not have a semantic phonological component i.e., are purely graphical^[43] and, therefore, become active when presented with basic line configurations. Moreover, the activation for such “meaningless” stimuli also occurs in the left hemisphere where VWFA is located. This means that activation of VWFA, apparently found by the symbolic proponents, cannot be assumed to be evidence of a symbolic or representational status for the early Blombos marks.

Similarly, activation of VWFA can occur, not because of a symbolic or representational propensity, rather it stems from the distilled perceptual properties of the patterns concerned. For example, Tanaka^[44] refers to such pared down configurations, including ‘T’ junctions, crosses and intersections, as perceptual forms that can over stimulate the visual system even though they only exhibit minimal features. Such configurations, in effect, encode important invariances that the visual system exploits to detect things in the world. Interestingly, Tanaka’s research was carried out on simians that lack a symbolic propensity in the sense implied by the symbolic model, yet activation to simple stimuli such as ‘T’ junctions and intersections were recorded in cells located in the inferotemporal cortex. Thus, EVC is crucial for assembling and integrating contour lines that signal edges and corners for the purpose of recognizing objects^[45], which signal ‘meaning’ in higher visual association areas but only in the sense that they point to coherent objects as processed by the left hemisphere^{[46][47]}.

The fact that abundant evidence from over two decades of neuroscience research has revealed how V1 and EVC constitute the first fundamental stage in contour integration—as well as a growing consensus reinforcing its role in quite sophisticated pattern recognition—underpins its relevance for understanding the way pattern perception in fossil humans was constrained by the same underlying cortical heuristics. This is commensurate with NRT’s claim that the earliest engravings parody the way information and pattern integration takes place in the early to later areas of the visual pathway in a way that encompasses feedforward and feedback dynamics—the balance which depends on ongoing task demands. In other words, the earliest engravings stimulate and simulate the way pattern perception is reciprocally assembled by the visual cortex from lower to higher areas.

Assimilating Diverse Results

Salagnon et al.^[3], in alluding to the relevance of V1 apropos NRT, state that:

This indicates that this region is not sensitive to the perceptual organization of the engravings, which contradicts the hypothesis that this region played a crucial role in the emergence of engraving production as it has been suggested.

Despite the definiteness of that statement, and considering the above reservations regarding the symbolic model, there are grounds for a consensus whereby the symbolic model can be incorporated into NRT, especially given the conclusion that:

...the issue is not the basic characters of the geometric shapes used to represent and convey symbolic meaning (which obviously are constrained by the fundamental properties of the visual cortex), but the way in which the brain re-organizes in order to connect specific kinds of visual shapes with either phonology or semantics (i.e., essentially a lexicon).^[4]

Yet, I would insist that the properties of the basic geometric configurations are as important as the semantics, not least because of the reciprocal interaction between semantic areas¹ in higher visual cortex with EVC, and the fact that visual information is filtered through EVC before it becomes liable to semantic attribution. After all, one needs initially to realize that there is something particular about a certain layout of marks before they can become the focus of semantics, which is exactly where a proto-aesthetic predisposition can provide the missing link. That predisposition seems to derive from the perceived ordered structure of different kinds of marks that *suggest* human agency, which may have been instigated by the mirror neuron system^[11].

The fact that the symbolic model is contradicted by numerous neuroscientific studies that demonstrate the importance of EVA and V1 for processing basic line features, and taking into account the above findings, this suggests that the incongruity may be due to the biases and limits inherent to fMRI. The possibility of attaining an integrated formulation was, however, tentatively suggested by Hodgson^[14] in an earlier riposte to the symbolic model. Similarly, Almeida^[48] regards the two approaches as complementary rather than antagonistic in recommending that the earliest marks should be regarded as stemming from a proto-aesthetic sense, with the same marks eventually attaining a proto-symbolic status, as originally proposed by Hodgson. Tylén et al.s'^[2] research also

confirms the relevance of a proto-aesthetic stage. Interestingly, Anderson^[49] independently came to the same conclusion as NRT by stating that:

Based on what we know of the plasticity of the visual cortex, repeated visual experiences of these environments may have heightened sensitivity, and visually nourished orientation cells in primary visual cortex V1 to respond more strongly to lines of particular orientation.

The possibility of reaching a compromise, however, has been impeded by the symbolic camp's reluctance to respond to the substantive neuroscientific evidence presented highlighting the role of EVC vis-à-vis early engravings^[14]—evidence that continues to call for a reply. This is in spite of the fact that the symbolic approach admits the involvement of EVC in the construction of pattern and form that precedes semantic/lexical attribution^[50].

Neuroesthetics and Neuroimaging

A crucial line of research that supports NRT concerns neuroimaging that has directly investigated the relationship between brain activity and aesthetic effects. Cela-Conde and associate's research^{[51][29]} is particularly relevant in that regard. Crucially, Cela-Conde and Ayala^[29] emphasize that it is essential to employ EEG or MEG, rather than fMRI, in order to identify aesthetic activation, which appears fairly rapidly following the appearance of an aesthetic stimulus. Interestingly, Cela-Conde et al^[52] found, using MEG, that aesthetic responses occurred in two stages, with the first phase involving perceptual correlates related to activation of early visual cortex (the initial aesthetic network) whereas the second appended the forward brain areas to the early occipital activation (delayed aesthetic network). Correspondingly, Vartanian and Goel^[53] used fMRI and found that the early visual cortex was active, together with higher forward areas, when subjects expressed a preference for abstract geometric patterns in paintings.

Those findings are supported by recent fMRI research where the procedure was structured to capture activation in the EVC in response to abstract configurations with many including patterns containing orientated lines, junctions, and edges^[54]. Fundamentally, that research found that the early visual areas, including V1 and V2, became active when such aesthetically pleasing abstract configurations were viewed. That outcome is referred to as 'significant configurations' that give rise to 'aesthetic perception.' With regard to NRT, those configurations are referred to as the 'elementary particles of

form’ or ‘graphic primitives;’^{[13][55]}. Furthermore, compared to neutral stimuli, those configurations —referred to as ‘artefactual beauty’— appear to be more potent in activating attention^[56]. Thus, even the early visual areas seem to be able to classify basic line configurations according to aesthetic criteria. Moreover, as with Cela-Conde and associates findings, Rasche et al^[54] established that the early visual areas correlate with higher visual areas (referred to as A1 involving medial orbitofrontal cortex and closely aligned areas) in response to aesthetical appealing abstract geometric patterns. In sum, early sensory areas in visual cortex play a foundational role in aesthetic experience even when this involves geometric configurations. This also aligns with NRT where the making of early repetitive patterns is referred to as a ‘proto-aesthetic’ tendency. Repetitive patterns may thus serve as a typical example of ‘cognitive affordances’^[57] because they effortlessly and fluidly interact with the way the early visual system functions.

Relevance of Neuroimaging and Scripts

The neuroscientific findings of reading and writing carried out by Dehaene and associates^{[58][59]} are frequently cited by those who support the symbolic model. By seeking to promote the symbolic thesis, however, they claim that Dehaene’s research demonstrates that the earliest engravings derive solely from cultural criteria by way of cultural evolution^[50]. In fact, Dehaene^[60] states just the opposite by asserting that numerous neuroscientific studies carried out by his team reveal certain biases of the visual system, which derive from evolutionary instantiated criteria and genetic factors, to the extent that such biases give rise to the ability to rapidly and efficiently decipher scripts (see Hodgson^[15] for a detailed review of this issue). In that sense, Hodgson^{[8][10][11]} demonstrates that those biases originate from a proto-aesthetic tendency relating to Gestalt principles of organization that arise from how EVC functions in tandem with the mesolimbic reward circuits of the brain, where the tendency is even observable in V1^[61]. In concrete terms, that interest seems to have been sparked off by the perceptual and motor skills required to make Acheulian tools, where the accidental scratches and score marks were either copied or added to in a way that produced coherent engraved patterns. That scenario is not entirely excluded by the symbolic supporters, as exemplified by the following statement:

Cut marks resulting from these activities often take the form of sets of juxtaposed or intersecting incisions. This utilitarian activity may have been crucial for the

development of the motor and cognitive skills necessary to produce durable, visible markings and to enhance their perception. Once the ability to produce such marks was in place, the next steps would have been to attribute some sort of meaning to them.^[4]

The symbolic model, however, sees that process as a leap from the skills required to make tools directly to symbol-making, when NRT suggests the necessity of an intermediary phase underpinned by a proto-aesthetic tendency conditioned by the satisfaction derived from producing finely-honed geometric tools. Thus, NRT^{[8][55][9]} first proposed that, because of the heightened perceptual ability and visuo-motor dexterity required for making Acheulian tools, accidental scratch or score marks will sometimes have approximated a pattern (including those produced by scraping or grinding to procure ochre or to prepare a surface e.g., Blombos and Klaisies River caves) which would have been noticed, thus providing a template for the intentionally engraved patterns. Butchery cut-marks may also be relevant here. As Hodgson stated:

..self-sufficient [intentional] marks could have derived from the accidentally produced scratches or cut marks created in the defleshing of bone or in the making and using of tools.^[8]

As well as Anderson mentioned above, Mackay and Welz^[62] make a similar point:

One possibility... is that scoring of ochre began as a means either of testing the suitability of the material to provide pigment or of increasing friction on a surface to be ground. Some scoring patterns may subsequently have become elaborate to the point at which design became an element of the process.

In similar vein, Parkington et al.^[63] state with regard to the Diepkloof eggshell engravings that:

Nevertheless, when according significance to marking, it seems reasonable to expect that some significance may have been given to objects naturally, rather than culturally, marked. Discrimination between similar objects can certainly reside in pre-existing, rather than intentionally produced, properties. These two observations remind us that what we are trying to reconstruct here are patterns of thought, not all of which manifest themselves unambiguously in the material record. The intentionally marked ostrich eggshell fragments from Diepkloof may reflect a pattern of thinking long practiced on other materials or with respect to natural markings.

Henshilwood et al.^[64], who support the symbolic model, allude to a similar principle in stating that an accidental made radial scar on a block from Blombos (piece M3-9), made in preparing the surface, was extended through the addition of an intentional engraving that created a dendritic motif.

Those insights point to the intimate relationship between the material world, the way it is transformed by human intervention, and the human perceptual-cognitive system. That interrelationship accords with material engagement theory where the material under transformation plays a transactional role in the first realization of external systems of information^[12]. Malafouris, although agreeing that NRT has potential as an explanation for the appearance of early marks, nevertheless, regards the theory as neurocentric. In fact, NRT stresses the importance of the materials undergoing transformation and the rapport of that process with cortical structures, as outlined above with regard to stone tool making and the heightened sensitivity to shape and form, as well as visuo-spatial manual skills, which arises thereby. From that perspective, I would submit that the first 'abstract' marks should be accorded a special status because they constitute an attempt at initiating an information system external to the brain^[65]; Bednark^[66] refers to such marks as "exograms". Consequently, they should be approached somewhat differently to other evidence of cultural behavior, such as ochre and personal ornaments that are often correlated with engravings by supporters of the symbolic model^{[3][50]}. Ultimately, we need to take into account the growing corpus of basic line engravings that attest to a geometric phase shared by a number of fossil humans, including Neanderthals, that stretches far back into the Middle Palaeolithic/Stone Age^[67]. The approach set out in this paper provides perhaps the most productive route to account for that phenomenon.

Conclusion

Although fMRI can provide a useful technique for ascertaining the significance of the earliest engravings, brain scanning results need to take the broader theoretical context into account. In addition, fMRI should be used in tandem with other brain scanning approaches, such as EEG and MEG, in order to arrive at a full picture of the time course and activity occurring along the visual cortex pathway. Furthermore, by demonstrating how tool-making and related activities are relevant (such as marks made in procuring ochre or cut-marks left in defleshing bones) in accordance with material engagement theory, research on understanding the first engravings would be in a much better place. By bringing those various strands together, a synthesis is possible that can potentially unify NRT, the

symbolic model, and material engagement theory in that the earliest marks, as proto-aesthetic precursors, provided the conditions that could be eventually exploited for ‘symbolic’ purposes.

Footnotes

¹ Semantics, in this context, refers to the visual system’s implicit ‘understanding’ of what an object or thing is or can do based purely on its visual characteristics i.e. its categorical features. This is different to what the symbolic model is referring to, which is to do with attaching a lexical meaning to abstract patterns. Neuroscience has established that verbal and visual semantic criteria can proceed independently but, unfortunately, are often confounded.

References

1. [^]Zeki S (1999). *Inner Vision*. Oxford: Oxford University Press.
2. ^{a, b, c}Tylén K, Fusaroli R, Rojo S, Heimann K, Fay N, Johannsen NN, Riede F, Lombard M. (2020). The evolution of early symbolic behavior in *Homo sapiens*. *Proceedings of the National Academy of Sciences of the United States of America* 117(9), 4578–4584.
3. ^{a, b, c}Salagnon M, d’Errico F, Mellet M. (2020). Neuroimaging and Neuroarchaeology: a Window on Cognitive Evolution. *Intellectica*, 2(73), 67–91.
4. ^{a, b, c}Mellet E, Colagè I, Bender A, Henshilwood CS, Hugdahl K, Lindstrøm TC, d’Errico F. (2019a). What processes sparked off symbolic representations? A reply to Hodgson and an alternative perspective. *Journal of Archaeological Science: Reports*, 28: 102043.
5. [^]Mellet E, Salagnon M, Majkic A, Cremona S, Joliot M, Jobard G, Mazoyer B, Tzourio-Mazoyer N, d’Errico F. (2019b). Neuroimaging supports the representational nature of the earliest human engravings. *Royal Society Open Science*, 6 (7), 190086. doi:10.1098/rsos.190086.
6. ^{a, b, c}Salagnon M, Cremona S, Joliot M, d’Errico F, Mellet E. (2022). Neural correlates of perceiving and interpreting engraved prehistoric patterns as human production: Effect of archaeological expertise. *PLoS ONE*, 17(8), e0271732. doi:10.1371/journal.pone.0271732.
7. [^]Salagon M. (2023). Emergence of symbolic thinking in humans: Investigating the neural bases involved in the perception of abstract Palaeolithic engravings and culturized faces using functional neuroimaging. *Bulletins et mémoires de la Société d’Anthropologie de Paris*, 35 (2). doi:10.4000/bmsap.12150.

8. ^{a, b, c, d}Hodgson D (2000). Art, Perception and Information Processing: An Evolutionary Perspective. *Rock Art Research*, 17 (1), 3–34.
9. ^{a, b}Hodgson D (2006). Understanding the Origins of Palaeoart: The Neurovisual Resonance Theory and Brain Functioning. *Paleoanthropology* <https://paleoanthropology.org/ojs/index.php/paleo/article/view/511>
10. ^{a, b}Hodgson D (2014). Decoding the Blombos Engravings, Shell Beads, and Diepkloof Ostrich Eggshell Patterns. *Cambridge Archaeological Journal*, 24(1), 57–69.
11. ^{a, b, c}Hodgson D (2016). Deciphering Patterns in the Archaeology of South Africa: The Neurovisual Resonance Theory. In T. Wynn & F. L. Coolidge (Eds.), *Formal Models in Evolutionary Cognitive Archaeology* pp. (133–156). New York: Oxford University Press.
12. ^{a, b}Malafouris L. (2021). Mark Making and Human Becoming. *Journal of Archaeological Method and Theory*, 28, 95–119. doi:10.1007/s10816-020-09504-4.
13. ^{a, b}Hodgson D (2019a). The origin, significance, and development of the earliest geometric patterns in the archaeological record. *Journal of Archaeological Science: Reports*, 24, 588–592. doi:10.1016/j.jasrep.2019.02.025
14. ^{a, b, c}Hodgson D (2019b). Response to the critique by Mellet et al. of Hodgson's Neurovisual Resonance Theory. *Journal of Archaeological Science: Reports*, 28, 102041.
15. ^{a, b}Hodgson D. (2023a). The Relevance of Geometry to Understanding Human Evolution from the Perspective of Cognitive Domains and the Neurovisual Resonance Theory.' In T. Wynn, K. A. Overmann and F. Coolidge (Eds.), *Oxford Handbook of Cognitive Archaeology (C17S1–C17N6)*. New York: Oxford Univ. Press.
16. ^aGarcía-Tabernero A, Peña-Melián A, Rosas A (2018). Primary visual cortex in Neanderthals as revealed from the occipital remains from the El Sidrón site, with emphasis on the new SD-2300 specimen. *Journal of Anatomy*, 233, 33–45.
17. ^aRehman A, Al Khalili Y. (2023). *Neuroanatomy, Occipital Lobe*. StatPearls Publishing.
18. ^{a, b}McManus JNJ, Li W, Gilbert CD. (2011). Adaptive shape processing in primary visual cortex. *Proceedings of the National Academy of Science U. S. A.*, 108, 9739–9746.
19. ^aReavis EA, Frank SM, Greenlee MW, Tse PU. (2016). Neural correlates of context dependent feature conjunction learning in visual search tasks. *Human Brain Mapping*, 37 (6), 2319–2330.
20. ^aGilbert CD, Li W (2012). Adult cortical visual plasticity. *Neuron*, 75, 250–264.
21. ^aGilbert CD, Sigman M, Crist RE (2001). The neural basis of perceptual learning. *Neuron*, 31, 681–697.

22. [△]Altmann CF, Bühlhoff HH, Kourtz Z (2003). Perceptual organization of local elements into global shapes in the human visual cortex. *Current Biology*, 13, 342–349.
23. [△], [△], [△], [△] Mijović B, De Vos M, Vanderperren K, Machilsen B, Sunaert S, Van Huffel S, Wagemans J. (2014). The dynamics of contour integration: A simultaneous EEG–fMRI study. *NeuroImage*, 88, 10–21.
24. [△]Martin AB, von der Heydt R. (2015). Spike synchrony reveals emergence of proto-objects in visual cortex. *Journal of Neuroscience*, 35 (17), 6860–6870.
25. [△]Chen M, Yan Y, Gong X, Gilbert CD, Liang H, Li W (2014). Incremental integration of global contours through interplay between visual cortical areas. *Neuron*, 82, 682–694.
26. [△]Chang CHC, Pallier C, Wu DH, Nakamura K, Jobert A, Kuo W-J, Dehaene S (2015). Adaptation of the human visual system to the statistics of letters and line configurations. *Neuroimage*. doi:10.1016/j.neuroimage.2015.07.028
27. [△]Chong E, Familiar AM, Shim WM (2016). Reconstructing representations of dynamic visual objects in early visual cortex. *Proceedings of the National Academy of Science U.S.A.*, 113 (5), 1453–1458.
28. [△], [△] Lee S, Mumford D, Romero R, Lamme AF. (1998). The role of the primary visual cortex in higher level vision. *Vision Research*. 38 (15–16), 2429–2454.
29. [△], [△], [△] Cela-Conde CJ, Ayala FJ (2018). Art and brain coevolution. *Progress in Brain Research*. 237, 41–60.
30. [△]Warbrick T (2022). EEG–fMRG: What we have learned and what does the future hold? *MDPI Sensors*. 22: 2262. doi:10.3390/s22062262.
31. [△], [△] Kosten L, Emmi SA, Missault S, Keliris GA. (2022). Combining magnetic resonance imaging with readout and/or perturbation of neural activity in animal models: Advantages and pitfalls. *Frontiers of Neuroscience*, 16. doi:10.3389/fnins.2022.938665.
32. [△]Itthipuripat S, Sprague TC, Serences JT. (2018). Reconciling fMRI and EEG indices of attentional modulations in human visual cortex. *bioRxiv preprint*. doi:10.1101/391193.
33. [△]Ress D, Heeger DJ. (2003). Neuronal correlates of perception in early visual cortex. *Nature Neuroscience*, 6, 414–420.
34. [△]Friston K (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society London. B. Biological Science*, 360, 815–836.
35. [△], [△] Kok P, de Lange FP. (2014). Shape Perception Simultaneously Up- and Downregulates Neural Activity in the Primary Visual Cortex. *Current Biology*, 24, 1531–1535.
36. [△]Summerfield C, de Lange FP. (2014). Expectation in perceptual decision making: Neural and computational mechanisms. *Nature Reviews Neuroscience*, 15, 745–756.

37. [△]Logothetis NK, Pfeuffer J. (2004). On the nature of the BOLD fMRI contrast mechanism. *Magnetic Resonance Imaging*, 22(10), 1517–1531.
38. [△][△]Murray SO, Kersten D, Olshausen BA, Schrater P, Woods DL. (2002). Shape perception reduces activity in human primary visual cortex. *Proceedings of the National Academy of Science U.S.A.*, 99, 15164–15169. doi:10.1073/pnas.192579399.
39. [△]Fang F, Kersten D, Murray SO (2008). Perceptual grouping and inverse fMRI activity patterns in human visual cortex. *Journal of Vision*, 8(7), 2–9, doi:10.1167/8.7.2.
40. [△]Murray SO, Schrater P, Kersten D. (2004). Perceptual grouping and the interactions between visual cortical areas. *Neural Networks*. 17(5/6), 695–705. doi:10.1016/j.neunet.2004.03.010.
41. [△]Geisler WS (2008). Visual perception and the statistical properties of natural scenes. *Annual Review of Psychology*, 59, 167–192.
42. [△]Wagemans J, Elder JH, Kubovy M, Palmer SE, Peterson MA, Singh M, von der Heydt R (2012). A century of Gestalt psychology in visual perception: I. Perceptual grouping and figure–ground organization. *Psychological Bulletin*. 138: 1172–1217.
43. [△]Reinke K, Fernandes M, Schwindt G, O'Craven K, Grady CL. (2008). Functional specificity of the visual word form area: general activation for words and symbols but specific network activation for words. *Brain and Language*. 104(2):180–9. doi: 10.1016/j.bandl.2007.04.006.
44. [△]Tanaka K. (2003). Columns for Complex Visual Object Features in the Inferotemporal Cortex: Clustering of Cells with Similar but Slightly Different Stimulus Selectivities. *Cerebral Cortex*, 13(90–99), 1047–3211.
45. [△]Wei H, Dong Z (2016). Contour representation and shape matching based on mechanism of visual cortex. 2016 International Joint Conference on Neural Networks (IJCNN), Vancouver, BC, Canada. 5014–5020. doi:10.1109/IJCNN.2016.7727860.
46. [△]Warrington EK, Taylor AM (1978). Two categorical stages of object perception. *Perception*. 7: 695–705.
47. [△]Warrington EH (2009). Warrington and Taylor's 1978 paper: Author's update. *Perception*. 38: 933–947.
48. [△]Almeida M (2023). From scratches to geometric figures: proto-aesthetics or proto-symbols? Visions of Neuroscience. *Anais – Seminário Nacional de História da Matemática I(15)*. <https://snhm.com.br/anais/article/view/11>
49. [△]Anderson H (2012). Crossing the Line: The Early Expression of Pattern in Middle Stone Age Africa. *Journal of World Prehistory* 25, 183–204. doi:10.1007/s10963-012-9061-2

50. ^{a, b, c}d'Errico F, Colagè I (2018). Cultural exaptation and cultural neural reuse: A mechanism for the emergence of modern culture and behavior. *Biological Theory*, 13, 213–227.
51. ^ΔCela-Conde CJ, Agnati L, Huston JP, Mora F, Nadal M (2011). The neural foundations of aesthetic appreciation. *Progress in Neurobiology*, 94(1), 39–48.
52. ^ΔCela-Conde CJ, Garcia-Prieto J, Ramasco JJ, Mirasso CR, Bajo R, Munar E, Flexas A, Del-Pozo AF, Maestú F (2013). Dynamics of brain networks in the aesthetic appreciation. *Proceedings of the National Academy of Sciences*, 110, 10454 – 10461.
53. ^ΔVartanian O, Goel V (2004). Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport*, 15: 893–897.
54. ^{a, b}Rasche SE, Beyh A, Paolini M, Zeki S. (2023). The neural determinants of abstract beauty. *European Journal of Neuroscience*, 57(4), 633–645.
55. ^{a, b}Hodgson D (2003). Primitives in palaeoart and the visual brain: The building-blocks of representation in art and perception. *Rock Art Research*, 20(2), 116–117.
56. ^ΔZeki S (2013). Clive Bell's 'Significant Form' and the neurobiology of aesthetics. *Frontiers in Human Neuroscience*. 7: 730. doi:10.3389/fnhum.2013.00730.
57. ^ΔTylén K, Hussain ST, Velliky E, Gonzalez RM, Straffon LM (2024). Honing Tools of the Mind: A Dynamic Framework for the Study of Symbolic Behavior in Early Human Evolution. *PsyArXiv*. doi:10.31234/osf.io/b8fz2.
58. ^ΔDehaene S, Cohen L, Sigman M, Vinckier F (2005). The neural code for written words: a proposal. *Trends in Cognitive Science*. 9, 335–341.
59. ^ΔDehaene S, Cohen L (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Science*, 15 (6), 254–262.
60. ^ΔDehaene S (2009). *Reading in the brain: The new science of how we read*. London: Penguin.
61. ^ΔSkov M. (2019). *Aesthetic Appreciation: The View from Neuroimaging*. *Empirical Studies of the Art*, 37 (2), 220–248.
62. ^ΔMackay A, Welz A. (2008). Engraved ochre from a Middle Stone Age context at Klein Kliphuis in the Western Cape of South Africa. *Journal of Archaeological Science*, 35:1521–1532.
63. ^ΔParkington J, Poggenpoel C, Rigaud JP, Texier PJ. (2005). From tools to symbols: the behavioural context of intentionally marked ostrich eggshell from Diepkloof, Western Cape. In F. d'Errico and L. Backwell (Eds.), *From Tools to Symbols: From Early Hominids to Modern Humans* (475–491). Johannesburg: Witwatersrand Univ. Press.

64. [^]Henshilwood CS, d’Errico F, Watts I (2009). Engraved ochres from the Middle Stone Age levels at Blombos Cave, South Africa. *Journal of Human Evolution*, 57(1), 27–47.
65. [^]Hodgson D. (2023b). *From Deep Patterns to the Origin of Writing and Information Systems: How Information Escaped from the Brain*. Barnes & Noble: New York. KDPAmazon Publishing.
66. [^]Bednarik RG (2014). Exograms. *Rock Art Research*. 31(1): 47–62.
67. [^]Hodgson D, Pettitt P. (2018). The origins of iconic depictions: a falsifiable model derived from the visual science of Palaeolithic cave art and world rock art. *Cambridge Archaeological Journal*. 28, 591–612. doi:10.1017/S0959774318000227.

Declarations

Funding: No specific funding was received for this work.

Potential competing interests: No potential competing interests to declare.