Understanding the Origins of Paleoart: The Neurovisual Resonance Theory and Brain Functioning

DEREK HODGSON

2 Belle Vue Street, York YO10 5AY, UNITED KINGDOM

ABSTRACT

Mark making on a range of objects and the manufacture of artifacts seem to have an ancient derivation, predating the representational depiction of the Upper Paleolithic by a considerable period. In an attempt to provide a coherent explanation for the appearance and longevity of these items, I submit a theory based upon how the visual cortex and visuo-spatial areas of the brain function in relation to the emergence of symmetry in lithic technologies. This theory endeavors to show how the preference of hominins for natural occurring objects, such as crystals and fossils, and the ability to make sculptured items, can potentially be accommodated under the aegis of one all-embracing explanation. It shows how various parts of the visual brain have influenced the preference for certain marks and shapes in that different regions of the visual pathways are shown to resonate or respond disproportionately according to the nature of the stimulus. These preferences are deemed to have become subject to material realization thanks to the interfacing of visual and visuo-motor pathways that had previously functioned as relatively separate systems.

INTRODUCTION

 $T\ensuremath{\mathsf{he}}$ cognitive abilities and behavioral profile of hominins are embodied in two main theories. One proposes a relatively rapid onset beginning some 40,000 years ago with the appearance various artifacts and cave art (e.g., Davidson and Noble 1989; Mithen 1996; Klein 1995, 2000; White 1989, 1992) whereas the second takes a longer more gradual, cumulative position (e.g., Bahn and Vertut 1997; Bednarik 2003a; Henshilwood and Marean 2003; Hodgson 2000a; Hodgson and Helvenston 2006; McBrearty and Brooks 2000). Short range supporters of the "standard model" tend to regard the appearance of modern human traits as a qualitative shift stemming from some rapid modification in brain organisation. The long range gradualists, however, see brain reorganization, and consequent behavioral markers, as proceeding relatively slowly over a long period well before the purported 40,000 bp boundary. This threshold is regarded as artificial due to the fact that as we progress further back in time the archaeology becomes diluted. There recently has been, however, a spate of artifacts and marks appearing well before the Upper Paleolithic for which the sudden onset approach is unable to account. What follows is an attempt to demonstrate how these divergent finds can be linked in a way that suggests that they may not be "one offs" with little consequence for understanding the cognitive behavior of hominins.

There is accumulating evidence that mark making, in the form of simple lines and geometric shapes, may be much more archaic than was at first thought (Bednarik 2003a). Geometrics, as they are sometimes called, are also a common and perplexing feature of the Upper Paleolithic, both in caves and on manuports. Although still the subject of controversy, marks of this genre may date as far back as 250,000 to 350,000 bp (Bednarik 1995a). Indeed, the archaic nature of these basic forms has recently received some confirmation in the authenticated geometric patterns issuing from Blombos (South Africa), dating to 77,000 bp (Henshilwood et al. 2002). Despite the discovery of Chauvet, which dates to around 32,000 bp, the products of which constitute the earliest representational *two-dimensional* images, there appears to be an excessively long period where representational forms are absent, yet simple repetitive lines and geometric shapes prevail. Interestingly, there is some evidence that 3D representations, in the form of sculptural-like objects, have an equally archaic provenance.

The fundamental question arises: why do graphic primitives appear to predate 2D representational images by such a long period? Logically, one would expect representational depiction to predate geometric motifs as the former would, to archaic humans, have had more of an obvious relevance and appeal than the latter. And objects are readily available in the natural environment that can be easily copied, whereas geometric shapes tend to be a rare to almost non-existent commodity. Furthermore, it would have been just as easy to produce a representational as a geometric figure by employing just a few simple lines, e.g., human stick figures, etc. Moreover, the similarity of these marks over a considerable period of time and place demands an explanation that does not depend uniquely on socio-cultural factors. Those hominins responsible for producing geometrics may not have been aware of the underlying reasons why they initially resorted to their creation, although they may have sought to project a significance of one kind or another. The focus of concern in this paper, however, will be with the underlying causes that motivated hominins to first start making geometrics rather than with how they might have been interpreted by their authors.

PaleoAnthropology 2006: 54–67. Copyright © 2006 PaleoAnthropology Society. All rights reserved.

THE NATURE OF EARLY MARKS

Some commentators (see Balter 2002) suggest that early marks may be nothing more than a kind of doodling. The precise geometric patterns and obvious symmetry, however, suggest that they derive from somewhat more than an absent-minded preoccupation. Moreover, the fact that nearly all of the marks so far discovered have been engraved onto relatively hard surfaces, such as rock, bone, and ochre, suggests the need for controlled and considered hand-eye coordination, which is not a typical characteristic of doodling. Of course, it is obvious that only the most durable surfaces survive the long periods involved (Bednarik 1994, 1995b)—so although softer material, such as clay, wood, etc., may also have been employed, the very fact that hard surfaces were exploited at all lends credence to the notion of an "intentional" origin.

In relation to the Blombos evidence, d'Errico et al. (2001) and Henshilwood et al. (2002) show how the surface of the objects concerned are scored with a number of diagonal and parallel lines. The lithic point used to produce these marks would have required enough control to ensure that the engraved lines ran parallel. In addition, the relatively small scale of the designs implies a considerable amount of fine motor-control involving a degree of concentration. This is supported by the fact that artifact SAM-AA 8938 has what appears to be an attempted straight line that spans the entire length of the object-this seems to bisect the central angle of the cross-like forms and is skirted by a border-like line at the top and bottom of the design. Furthermore, there is substantial evidence of surface preparation of the ochre pieces, with indications of a similarity in engraving technique and design, which suggests a deliberate sequence of repeated events (Henshilwood et al. 2002). These observations argue strongly against any suggestion the authors were merely concerned with doodling. "Doodling," it should be added, is too imprecise a term to be used in this context as it merely refers to a certain lack of concentration and intention to the marks produced. Doodling-like marks can be produced even when there has been much attention and effort in their making (young children, for example, produce such marks, towards which they display much concern).

Henshilwood et al. (2002) and d'Errico et al. (2001) propose that the Blombos finds may have had a symbolic function in the inherent decorative appeal as a sign of group affiliation. This explanation, however, seems to assume that which it seeks to explain, as the precise mechanism responsible for the production of these marks remains to be established. Here we have to be careful about what is meant by symbolic. The notion that the Blombos marks might be of this genre has to be seen in the context of what a "sign of group affiliation" implies. This certainly does not mean that they were symbolic in the sense that there is a specific convention employed, where the symbol, as an abstract shape, has an arbitrary relationship to the intended referent as part of a multifaceted semantic network of denotations. To learn true symbols we begin by learning symbol-object correlations, but once learned, these associations must be

treated as no more than clues for determining the more crucial relationships which are not highly correlated—in fact, just the reverse. In short, the actual meaning becomes embedded within a complex structure of inter-relationship associated with a rich interplay of other referents.

What, therefore, might be the more probable, but parsimonious, frame of reference appropriate to an explanation pertaining to early geometric marks? Deacon (1998) suggests that an indexical relationship based on a conditioned response, as a lower-order contingency, can explain many of the communication systems in primates and mammals. Thus, the scent laid down by animals, such as wolves, to ward off competing packs is an indexical sign of territory because the latter have learnt, through association, that this scent means trouble. The same scent for those defending the territory, however, becomes an index of security because, for these wolves, the defended area has become synonymous with the preservation of food resources and the safety that comes with group solidarity. This has much in common with the concept of group affiliation that Henshilwood et al. (2002) propose as an explanation for the appearance of the Blombos marks. In sum, the appropriate level of explanation for considering early marks may be indexical or associative rather than symbolic in the stricter sense of the term. The term "sign," as referred to in this context, should therefore be interpreted according to this definition. In this respect, the early visual cortex has diminished in size relative to non-human primates yet the human brain possesses a considerable number of higher level visual and visuo-motor association areas, a process that seems to have begun with the australopithecines (Holloway et al. 2001). It is thought that the expansion of the higher visual areas may have occurred at the expense of the olfactory sense when the common ancestor to apes, a nocturnal animal, became a diurnal forager (Falk 2006). This suggests that hominins were using their highly refined visual capacities coupled with increasing motor control to realise, in material form, visual coordinates as indexical signs.

But even if these marks were a sign of group affiliation as a means of delineating territory in the face of competing groups, this still does not explain how they first came about and how meaning was eventually attributed to them. There is the further problem of universality. Group affiliation as an explanation would, by definition, predict a considerable variation in motifs throughout the archaeological record but this seems not to be in evidence (Bednarik 2003a). The motivation that first led to their initial production therefore still remains the key question to be answered.

In the absence of any representational clue or direct evidence of intent, it is difficult to quantify exactly what marks of this order signified to their makers. Fundamentally, before repetitive lines became imbued with decorative (or any other) significance they must have existed as marks in themselves—what Davis (1986, 1992) refers to as "selfsufficient marks." Their similarity throughout time and place indicates that there may be a common pre-determining mechanism at work here. Given this, are we then able to go on and say anything about the nature of the mechanism involved? That the marks have such an ancient derivation and are long-lasting suggests inborn factors may be relevant. This is supported by the fact that when infants, the world over, first begin to draw they produce similar types of repetitive marks (Cox 2005) and comparable marks are produced by modern humans (Dronfield 1996). A limited number of similar graphic primitives have also been observed in the drawings of chimpanzees that seem to take a spontaneous interest in dots, lines, and curves without the need for any extraneous reinforcement (Tanaka et al. 2003).

It seems the "aesthetic" interest in geometric primitives arises from the fact that pleasure is gained from viewing purified and concentrated versions of such patterns, arousing a sense of satisfaction. It is exactly the same types of motifs that vision researchers have found that early analysers in the visual cortex lock onto as they endeavor to make sense of visual reality. Straight parallel lines, curves, and right angles embody some of the main nonaccidental properties the visual system seeks out because they are decisive indicators of the existence of solid objects in the world. Repetitions of a pattern usually derive from a unitary source such as a tree trunk, a rock face, or a body of water, etc. (Pinker 1997). This embodies the Gestalt principle that similar looking items group together and is probably realised in early neural centers by neurons firing in synchrony, i.e., what fires together goes together (Hebb 1949). These factors are sufficient to explain how and why repetitive motifs were the first to be realised and became so widespread in the decorative arts in almost all cultures (more on this below).

THE UNDERLYING NEUROPHYSIOLOGICAL MECHANISMS—RESONANCE AND THE EARLY VISUAL CORTEX

Elsewhere, I have advocated that the early areas of the visual cortex may be the crucial region of the brain responsible for the sensitivity to repetitive patterns (Hodgson 2000a, 2000b, 2003). In order to understand the relevance of the visual cortex in this respect, it is necessary briefly to outline the basic structure and functioning of this part of the brain. In general terms, it is composed of several hierarchical layers, each layer of which is thought to process incoming information, beginning with simple components and gradual moving through subsequent levels to accommodate more complex shapes (Figure 1). The first major area involved in this process is V1 (primary visual cortex), an area devoted to dealing with the most rudimentary kinds of visual information (e.g., simple lines and dots). At the next major area, V2, lines are assembled together to make more coherent shapes after which V4 appears to assimilate these to apportion figure and ground. Much of the "computation" performed at these early levels is about constructing the image and is viewer-centered (based on the actual object). From early areas, visual information is transferred to the inferotemporal cortex where recognition takes place and is object-centered (based on templates that provide constancy despite change). There is also much feedback from higher

to lower areas that serves, amongst other things, to enhance perception.

What I am proposing is the hypothesis that the chronology by which geometric primitives turn up in the archaeological record—from simple lines to more complex forms and, ultimately, in the Upper Paleolithic, geometrics and representation of animals—may be analogous to how the brain constructs form. This might seem more feasible when it is realised that specific areas of the cortex would have been involved in the actual perceptual processes giving rise to mark making. Consequently, the eventual production of figurative depiction might, of necessity, require a stage of graphic primitives as a preliminary. I call this the "neurovisual resonance theory" of mark making, as it expresses the way mark making both simulates and stimulates the process by which the visual system constructs form from primitives and how the two functions are reciprocal. Put another way, I propose, as a result of biological evolution and individual learning, that an organism is, at any given moment, tuned to resonate to incoming patterns of the optical array corresponding to the invariants that are significant to it. On perceiving repetitive-like patterns, the early visual centers are thought to become hyper-stimulated, leading to an undifferentiated sense of arousal, due to the fact that the early visual areas are already pre-tuned to be responsive to such lines because they play such an important role in discrimination of objects in the world at large. This may explain why infants first begin to create geometric-like shapes and repetitive marks before representational forms-from 18 months to 3 years of age when the early visual cortex is already fully formed in contrast to the higher visual and visuo-spatial areas (Casey et al. 2005). The same applies to chimpanzee drawings and visual areas, except V1 and V2 continue to be predominant.

The pervasiveness and primacy of geometric marks over representational depiction may therefore reside in a rudimentary "aesthetic" sensibility that is premised on V1 and V2 as the "gatekeeper" to higher visual areas (Tootell et al. 1998). Moreover, the early visual cortex is activated twice over, once when one perceives an object and again when one needs to scrutinize things in more detail-as well as when mental imagery is required. When we look at simple lines, the activation of primary visual cortex is accentuated, but when observing objects, both V1/V2 and the inferotemporal cortex are activated. When looking at a picture of an object, we are not actually seeing the object but a surface covered in abstract marks and shapes. So the early part of the visual cortex would automatically be stimulated together with higher areas. The response of the individual to these contingencies will not be realized consciously but will be based on the "aesthetic" response, as outlined. For example, infants and chimpanzees when drawing simple shapes are unaware why they produce such motifs but nevertheless take great pleasure in their production. The same factors may have been crucial to the making of early marks and help to explain why they pre-empted representation and why they are so prevalent in tribal and ethnic art, as well as more generally.



To make this idea more explicit, a tuned resonator involves constraints in the sense that the particular tuning of a resonator will lead that unit to respond maximally only when a stimulus that perfectly matches its tuning characteristics is perceived (see Shepard [1984] for a summary of this approach). Figure 2, for example, shows how neurons in V2 (the second major area for processing form after V1) are predisposed or tuned to respond maximally to certain basic geometric shapes (Hegdé and Van Essen 2000). This example illustrates how two separate neurons in V2 are tuned to respond only to specific kinds of geometric stimuli, in this case curved forms, such as concentric circles and spirals, and angles composed of straight lines. In other words, this part of the visual brain contains neurons that are specialised for processing different kinds of geometric shapes in that they have a particular resonance to these shapes. A resonating system can have different modes of excitation in that the same tuning response may be activated in various ways. In the present context, this means the system can be activated by external stimulation such as a micro-electrode, drug-induced states, or, more fundamentally, simply through straightforward perception of repetitive lines and geometric shapes, as is found in early art. Figure 2, when compared to Figure 3, illustrates the remarkable similarity of neural primitives to Lower/Middle Paleolithic geometric marks providing compelling evidence that they may indeed stem from how the early visual cortex functions.

Although it is possible to find straight lines or geometric shapes in the natural environment, e.g., horizon lines, strata, celestial bodies, ripples, etc., these are the exception rather than the rule, as the natural world is dominated by apparent confusion. By producing geometric marks in graphic form, the effect of such natural distractions would have been greatly diminished, thus increasing their potency leading to more effective resonance of tuned mechanisms in the early visual system. Crucially, natural scenes also



Figure 2. Showing how two separate neurons in V2 respond preferentially to particular kinds of geometric forms A. Right angles and B. Concentric circles (concentric circles are often mistaken for spirals and vice versa). The red (positive) through to blue (negative) colour scale indicates extent of preference. Note that the tuning of these cells is graded in the sense that they also fire with stimuli that are close to their best option. This may be a means whereby the overlapping tuning curves of each neuron serves as an efficient way of encoding a broad range of shapes with a limited number of cells. The bar charts present the same information in a different format. (Hegdé and Van Essen 2000: Figure 1)(Reproduced with permission of authors and The Journal of Neuroscience ©).



Figure 3. Some of the typical motifs and patterns (geometric primitives) from the Lower to Middle Palaeolithic. These marks are also abundant during the Upper Palaeolithic and 'art' of subsequent periods.

have embedded within them line segments and contrast edges that V1 seems especially suited to deal with; these remain unavailable to later visual areas (Lamme and Sperreijse 2000)—in this sense such lines have become reflected in the structure of the early visual cortex. Accordingly, mark making, through the hierarchical process indicated, would have served as a way of stimulating neurophysiological substrates because they accentuate these embedded line primitives—thus leading to the depiction of form constants. The precise chronology of this activation will be discussed presently.

EVIDENCE FOR A DIRECT RELATIONSHIP BETWEEN THE VISUAL CORTEX AND EARLY MARK MAKING

As the early visual pathways have evolved to detect certain invariances relating to order and symmetry embodied by line, edge, and angle, these stimuli resonate more at lower levels. This is due to the fact that this early area has a raised sensitivity to the presence of lines (Zeki 1999). Kunst-Wilson and Zajonc (1980), for example, have demonstrated that when geometric forms are presented at such a rapid rate that only a flash can be discerned, when the same shapes (together with an array of similar but slightly different shapes) were subsequently presented at a slower, easily recognisable rate, the originally presented forms were reliably discriminated by subjects. As the initial forms were not consciously perceived, this discrimination was found to be based on an affective response or indeterminate sense of arousal in humans (see also Berlyne [1960, 1971] and Hamilton-Smith [1986]). Kunst-Wilson and Zajonc (1980) concluded that there are partially independent systems encoding affect and content of which the former is mediated by pre-conscious determinants.

The relationship between geometric forms and emotional-arousal suggests that the preference for such shapes may be underwritten by pre/subconscious processes that we are not always privy to, yet which can still determine behavior. This mechanism might very well underpin the attraction humans seem to have for geometric forms (see, for example, Bando 2000). In other words, when humans see simple shapes and forms or orderly arrangements they tend to be attracted to them and focus on their qualities. By so doing, they increase attention/arousal levels thereby producing greater demands on the visual system. One of the main effects of this is to stimulate areas V1 and V2 which, as well as encoding such geometric primitives, are also involved in tasks that require greater attention to and close scrutiny of fine detail (Ress et al. 2000). Furthermore, the sensitivity of neurons in these areas is also known to increase as a result of training or practice (Li et al. 2004; Schoups et al. 2001). This suggests the existence of a feedback loop whereby the activity of producing geometric marks helps to fine tune neurons in the early parts of the visual cortex necessary for the rapid discrimination of things in the world. This is a self-generating feedback loop without the need for any extraneous reward because, as we have seen, producing marks of this kind is self-rewarding by way of, what I would argue, are the various dynamics contained in early visual cortex. Recently it has been confirmed that V1 may be more implicated in visual attention, awareness, and focal attention than was previously thought by way of helping to enhance the salience of objects in certain conditions, e.g., "pop out" figures (Lamme and Sperreijse 2000). This involves feedback from higher visual areas to V1 that illustrates how this area can perform a dual, if not multipurpose, role in picture perception as implied above.

Importantly, various studies have shown how these early areas are fundamental to the experience of phosphene-like forms. For example, Bressloff et al. (2000) have confirmed that the structure and functional correlates of V1 (and V2) can be modelled mathematically to the extent that the same (or similar) forms as phosphenes have been found to arise as a result. This study is important because it is an objective demonstration of how the architecture of V1 - V2 gives rise to phosphene-like forms. Importantly, phosphenes evince surprising similarities with marks from the Lower to Middle Paleolithic (Bednarik 1984, 1986b, 1990).

Additionally, it seems that animals as well as humans (Appelle 1972; Furmanski and Engel 2000) are preferentially tuned to horizontal and vertical lines because the neurons encoding such lines are more widely distributed in the earlier parts of the visual cortex than subsequent areas. This proclivity is thought to stem from the fact that natural scenes incorporate more vertical and horizontal lines than any other, though this might not seem obvious to the ordinary eye (Dragoi et al. 2001). In later areas, however, oblique lines are represented just as much as horizontal and vertical ones. This has led to the finding that humans are better at resolving and discriminating vertical and horizontal lines in many different kinds of perceptual tasks, yet individuals remain unaware as to the reality of this effect (Berkley et al. 1975; Essock 1982). It may also explain why children find it easier to draw horizontal and vertical lines than oblique ones (Ibbotson and Bryant 1976).

Zeki (1999) suggests that none of the early visual areas, including V1, merely serve to relay signals to other areas, instead each region actively transforms the incoming signals and may contribute explicitly, if incompletely, to perception. This will include later areas of the early visual system such as V4 (implicated in discriminating figure from ground), and an area known as the middle occipital gyrus (MOG) thought to be particularly involved in symmetry extraction (Tyler 2000; Tyler et al. 1998). Tyler et al. (1998) make the further point that the symmetry-specific responses observed in MOG imply the existence of neurons with large receptive fields that are *driven* by patterns of activity spread across the mosaic of neurons in earlier visual areas

One interesting observation may be a pointer to the importance of these factors in this context. There seem to be no examples of representational art without an accompanying geometric tradition in indigenous groups, yet we often find geometric tradition without representational art, e.g., the Songe of New Guinea. This is not to say that those groups lacking a tradition of representation do not possess the potential to produce such-circumstances or environmental factors may simply be adverse to their production. Geometric art is pervasive in native communities throughout the world and the criteria cited regarding the visual cortex may help to explain this. Additionally, it demonstrates that the making of geometrics may be a more accessible process than the making of representational motifs. This is substantiated by the fact that an Amazonian Indigene Group with no tradition of geometric spatial concepts has been found to spontaneously understand the contingencies appertaining to points, lines, parallelism, and right angles in a search task, suggesting that knowledge of geometrics may be "innate" (Dehaene et al. 2006). Importantly, this group had no schooling or artifacts that may have aided them in this task.

THE EVOLUTIONARY PREDETERMINATES OF SYMMETRY AND REPEATED LINES

Helvenston and Bahn (2003) highlight the fact that the proclivity to perceive geometric figures was hard-wired into the primate brain millions of years ago. The preference for order, repetition, and geometric patterns in both animals and humans may therefore arise from certain long-standing determinants, relating to their importance for detecting form in various situations, as a means of holding constant the flux of the world so that objects can be reliably perceived. Geometric shapes in patterns embody this kind of scenario in that, as repeated motifs, they remain a stable enduring commodity.

When we find simple geometric patterns in nature, then, as a species, we are apt to think something profound has transpired. Our minds are therefore instruments with a particular preference for simple geometry that probably reflects the architecture of the visual brain. Indeed, Richards (1971) even went so far as to suggest that certain form primitives are a consequence of how the neural structure of the visual brain fits together, in hexagonal columns, as a means of tightly packing components into a limited space—and this is a product of how nature has "solved" this kind of problem as exemplified in natural systems of growth.

Thus, it can be said that during evolution there has been a reciprocal interaction between cognitive mechanisms and the regularities of the world (Shepard 1984: 434; Tooby and Cosmides 1992: 72). In other words, many statistical and structural relationships that endured across human evolution were "detected" by natural selection, which designed corresponding computational machinery specialized to use these regularities to generate knowledge and decisions that would have been adaptive in the environment in which humans evolved (Cosmides and Tooby 1994). Therefore, repeating patterns will tend to evoke extensive excitation in neural circuits because of the very fact they are self-congruent. Massive neuronal resonance to symmetry and pattern may be a function of a deep internalisation of the abstract principles of transformational geometry. Such resonant circuits in the early visual cortex may, hence, spontaneously "reverberate" when presented with particular patterns or forms that approximate early neural centers. The creation of repetitive patterns as well as simulating the processes by which form is generated in the early visual areas, may also be a way of honing perceptual and visuo-motor skills, as well as promoting increased awareness to environmental signals (nonaccidental properties) with accordingly greater survival rates for those so disposed. They could also be described as an exaptation deriving from the correlates contained in the early visual cortex.

The making of Lower and Middle Paleolithic marks would have necessitated some feeling for visual order, sharp linear precision, regularity, and control. It was thanks to the "guiding hand" of the early visual cortex, as cited in the foregoing, that this competence came to be realised. In a world full of insecurity and sudden dangers, such marks may subsequently have come to represent more overtly the qualities of order, regularity, and control, but this continued to be mediated by the way in which the inherent structure of the early visual cortex came to actualize certain invariance in response to adaptive needs. Sensitivity to repeated symmetry will have been selected for because simple features of this type have special status in the perception of form and, therefore, for the detection of objects in the environment essential for survival (Vetter et al. 1994).

This sensitivity may have evolved because it is crucial for discriminating living organisms from inanimate objects. Most biologically important objects, such as predator, prey, or mate are symmetrical. Symmetry thereby serves as an early warning system that serves to direct the visual system to facilitate further processing of the object in question until it is fully recognised (Ramachandran and Hirstein 1999; Tyler 2000). Contrast extraction also takes place before overt recognition and together with grouping, in the form of pattern and texture, can lead to the facilitation of borders between regions and the accentuation of surface areas. This aspect of perception is particularly significant because it can be used as a means of disambiguating the camouflage of predator and prey. Experiments with functional MRI imaging have demonstrated that humans are able to accurately discern symmetrical objects in less than a twentieth of a second and the eye is particularly fast at discerning objects with vertical mirror symmetry. The detection of symmetry, as Julesz (1981) has established, is therefore virtually automatic in that it precedes attention—the probable explanation for this residing in the fact that symmetry might be a characteristic of an advancing predator. And once symmetry has been detected, the eye will then only track parts of the object that have not yet been assimilated (Locher and Nodine 1987). In this respect, once a line of vertical mirror symmetry has been ascertained, the eye proceeds to explore only one half of the object because the other half is then taken as given. The question arises, however, how did this sensitivity to symmetry become translated into a material form? After all, nonhuman primates by necessity are also sensitive to symmetry for similar reasons as humans. This problem will be discussed in relation to stone tools in the next section.

Early marks were, therefore, not so much a badge of group affiliation but rather an acknowledgement of stability in the face of a hostile and uncertain environment. Repetitive marks and symmetrical patterns, as a contingency which reflects the way the human visual system holds constant certain aspects of the world in order to encode its enduring properties, would have spontaneously appealed to hominins by way of the aforementioned resonance. Because of this, these patterns would have been reproduced as a means of stimulating the sense of empathy and reassurance thereby afforded. As Arnheim (1971) proposes, an economical use of shape can establish a bit of order in a world of complexity and what appears at first sight to be a limited vocabulary of units may, in the discovery of similarity, represent a strength. Faulstich (1986) has made the important point that "art" may have begun as a means by which the gap between the natural order and the human order is bridged and, he goes on, early marks may have been an expression of "control, inter-relatedness, orderfinding and order-creating." In these terms, it is possible the present day universal inclination for decorative pattern may similarly stem from the original sense of equanimity in the face of the vagaries of nature as mediated by the concomitants typical of the early visual cortex.

In short, the reason repeated lines and geometric shapes are so appealing is not so much because of their rarity in nature, but more because they are already an integral feature of the brain. Geometric motifs were thus, for archaic humans, "self-sufficient marks" (Davis 1986) that were "good to think" (Harrod 2003) because they provided a measure of certainty and predictability in the face of unpredictability.

THE VISUAL CORTEX, VISUO-SPATIAL BRAIN, TOOL MAKING, AND SYMMETRY IN RELATION TO EARLY MARKS

The area of the brain responsible for recognising objects (the "what" system), although it has some similarities with the nonhuman primate, is nevertheless capable of processing greater amounts of information at a more sophisticated levels. This is verified by the fact that the former's sensitivity to form is more cue invariant (Denys et al. 2004) and, when stripped of its higher faculties, a modern human brain and behavior are not equivalent to that of a chimpanzee (Donald 1991). So, the human visual system in its "raw" state still has a greater ability to deal with, and sensitivity to, the recognition of objects.

Although this theory seeks to explain the reason why hominins were attracted to repetitive marks, it does not elucidate how this interest came to be translated into a proactive replication of their intrinsic appeal. Wynn (2002), Edwards (2003), Harrod (2003), and Feliks's (1998, 2003) views are particularly enlightening in this respect, especially with reference to the making of bifaces and stone tools. These commentators stress the fact that such implements show evidence of a design sense on the part of their makers that went someway beyond the purely practical and functional. It was not, however, the ability to make and shape symmetrical stone tools that led to the making of geometrics but the raised awareness that comes with a more sophisticated and developed visual memory which, as we shall see, came to interface with spatial/motor coordinates with greater efficacy. So, although the making of tools will have facilitated the expansion of the parietal areas, concerned with visuo/ motor skills and mental rotation (Hodgson, 2005) in hominins, once this had reached a certain level it would have occasioned the ability, not just to make regularly shaped stone bifaces, but also geometric marks. In other words, increased visuo/motor/spatial control allowed the more sophisticated visual processing in Homo heidelbergensis to be translated into a material form.

Wynn (2002), in particular, goes further by showing how shape constancy is fundamental to understanding both tool making and early repetitive marks. He argues that the production of bifaces with three-dimensional symmetry some 500,000 years ago is evidence that the spatial cognitive prerequisites for producing regular geometric marks were already in place. In proposing this idea, Wynn may have hit on the crucial dynamic that allows us to understand how geometric marks arose during the Lower to Middle Paleolithic. The fact that archaic humans may have been going beyond what was necessary in terms of the functional requirements of a tool is highly significant. This means that rather than just being a consequence of the cognitive capacity for spatial competence, they also became interested in the actual shape of the tool itself.

Recent findings in how the brain functions can help to clarify why this sequence evolved in this way. The visuo-spatial pathway (the "where/how" dorsal system) involving visually guided action, which would have been intimately involved in the making of tools, is thought to be "blind" (Goodale et al. 1991; Turnbull et al. 1997; Ungerleider and Mishkin 1982). In contrast, the "what" ventral pathway (for overt visual identification) may downplay or even completely ignore spatial coordinates because these are largely irrelevant for a recognition system that strives to achieve object constancy (Turnbull et al. 1997). However, visuo-spatial imperatives would be crucial if one decided to act on an object. The pathway for visually guided action is thought to culminate in the superior parietal lobe and as this area is deemed to have undergone enlargement from *Homo hablis* through *Homo erectus* to modern humans (Stout 2005; Stout et al. 2000), this has obvious implications for the present discussion. This may also be related to an increase in cerebral asymmetries and right-handedness

in *Homo erectus* (Holloway 1999). Interestingly, Stout et al. (2000) has shown that the superior parietal lobe tends to be particularly active when an experienced stone knapper fashions a tool.

The implication here is that the makers of tools in the late Acheulian were beginning to rely on the "what" system that identifies and brings objects to full conscious awareness, rather than, as in before this period, the "where/ how" pathway. In fact, the modern human inferotemporal cortex (part of the "what" system) has been found to have a privileged area devoted to the identification of tools (Caramazza and Mahon 2003), which may have sprung from the increased dependence, interest and benefits deriving from and attending to, the shape of bifaces. Therefore, before the late Acheulian, hominins would have been relying more on the "where/how" system but subsequently the "what" pathway began to figure more prominently in the equation. In fact, there is some persuasive evidence that in humans, in contrast to chimpanzees, there is a third pathway linking the normally separate "what" and "where/how" systems (Glover 2004; Hodgson 2005), thereby helping to improve hand-eye coordination essential to the making of finely shaped tools (see Figure 1). These observations parallel Wynn's contention that, before 500,000 bp, tool making was of a rudimentary quality compared to the subsequent step-change in expertise. This also coincides with Wynn's willingness to accept the idea that implicit knowledge may have been the determining factor in tool making before the late Acheulian but that the later three-dimensional congruent symmetries were mediated by other factors (Wynn 2002: 429). The foregoing analysis should help to clarify some of the cognitive substrates and processes that may be responsible for the later symmetries found in hand-axes.

Regular, repeated, symmetrical forms and patterns suggest a contingency that remains the same despite variation, which provides a clue as to how tool making can be related to early mark making. In this regard, Shepard (1990) proposes that symmetrical patterns constitute a component important for survival in that they embody symmetrical and spatially repeating elements of a visual input belonging to the same external object. This is self-similarity in the sense that, as an abstract pattern, it implicitly suggests stability in the face of fluctuations. More simply, despite the many variations an object might undergo due to change, something tells us it remains the same. It is this something, i.e., self-similarity, that a repeated pattern suggests. For example, a sphere has perfect self-similarity in that the same shape, a circle, defines the perceived outline through all rotations around its center. A more complicated form, such as a cube, though not congruent under certain rotations, becomes so (a repeated square) under certain angles of rotation (through multiples of 90° about the central axis). So, the perception and recognition of shape may itself be based on the implicit computation of the self-similarity of an object under all possible rigid transformations (Shepard 1990). This point is particularly important in relation to Wynn's assertion that shape constancy was already in place before stone tools were fabricated during the late Acheulian, in that there needed to be an awareness of self-similarity before the symmetry of a tool could be produced.

Given that hominins seemed to have had a precocious but "passive" appreciation of pattern and symmetry as manifest in the collection of and preference for crystals, fossils, etc. (Bednarik 2003a), the fact that this inclination came to be intentionally projected onto various surfaces is highly significant for understanding the rudiments of cognitive development during this period. The temporal cortex, concerned with recognition and visual memory, seems to have undergone expansion in humans (Joseph 1996), whereas, as has been noted, the early visual cortex has remained virtually the same, i.e., has diminished in size relative to later visual areas. This suggests that humans have a raised awareness to visual information coming from earlier occipital centers compared to nonhuman primates, which would explain the hominin proclivity for passive appreciation of natural occurring objects that have any accidental likeness to real objects as well as such things as fossils, shells, crystals, and geometric marks. Symmetry extraction is also important here, as Tyler's observation of a specific part of the early visual cortex devoted to this task suggests that humans will also have been more alert to any objects that embodied symmetry.

Hominins seemed to be able to take shape constancy, which allows the world to be seen in a stable and coherent way, and intentionally translate this into bifaces of prodigious symmetry. This amounts to an assimilation of a decisive perceptual contingency so that it can be realised, and subsequently reproduced, in a tangible object. This level of expertise would have quite easily lent itself to other processing formats, such as cupules (radial symmetry) and the making of repeated geometric forms and lines (translational symmetry where a pattern is repeated in sequence). The fact that the late Acheulian horizon overlaps with that of the first documented "intentional" marks (a meandering line and cupule), from Auditorium cave, Bhimbekta, India (c.500,000 to 200,000 bp) and other marks such as those from Bilzingsleben, substantiates this thesis. The setting of similar kinds of marks into assemblies of two or three clusters, often found in these cases (Bednarik n.d.), is an example of the classic Gestalt perceptual principle of grouping, as is the principle of good continuation where lines or dots are placed in parallel. Crucially, these principles, and others, (e.g., closure) are exploited by the perceptual system as clues that help define objects and may well be hard-wired in the visual system. Cupules, being circular, exemplify the principle of closure. Circularity is regarded as a key geometric by Arnheim (1974) that is referred to as the "primordial circle" – probably due to the fact that it is a relatively simple outline that economically divides figure from ground, i.e., the inner from the outer, and, in this respect, is a generalisation of an enduring feature of natural forms. The shadow cast within a cupule's boundary, when viewed from a distance, helps accentuate its circularity. From a distance, however, cupules will tend to appear as spots or dots, an early perceptual primitive. Interesting, they are often arranged in lines or clusters that accord with the notion of good continuation and grouping respectively. The Gestalt principles as applied to how marks are universally realised in two dimensions may be justifiably defined as "laws," as is the tendency to gravitate from simple to more complex lines and shapes (Arnheim 1974).

Interestingly, as is the case for tools during the same period, early marks betray a similar slow course of change over time. Repeated lines, net patterns, lattices, finger "macaronis," and arcs and circles, are all evidence of this as they are both widespread and archaic (see Bednarik, 1986a, 1986b, 1986c; Figure 3 here). So, the emergence of sapient behavior may well be evident in the transcending of a passive appreciation of symmetry and pattern, towards a more proactive exploitation of such components through actual mark making—at first, through a gradual, almost negligible, increase in varieties of shapes and forms, to a later more exponential increase with the arrival of later humans. This sequence seems to be reflected in the archaeological record, with early marks of a more rudimentary disposition—simple straight lines and curves often repeated in a series (Hodgson 2000a). Later geometrics, as are found in Upper Paleolithic cave art, seem to evince a greater range of shapes and motifs than those before this period suggesting a more sophisticated understanding and ability to improvise (see, for example, Conkey 1980).

Taking these observations into account, a likely explanation for the appearance of geometrics is to be found in the fact that, in the de-fleshing of bone and making of tools, scratch marks of various kinds will have been produced. Some will have accidentally assumed the configuration of a regular pattern and therefore became significant in the way described. This is corroborated by the fact that accidentally-made but regular cut marks, thought to have been made by *Homo heidelbergensis* as a consequence of systematically cutting fillets from animal carcasses, have been found on bones from Boxgrove, England (McKie 2000). In addition, a stone tool from Qafzeh Cave, dating to the Middle Paleolithic, shows evidence of possible intentionally engraved repetitive lines (Hovers et al. 1997). This explanation is more probable because the implement used to produce scratch/cut marks will have been conveniently at hand, so that a repetition of the initial procedure could easily have been re-enacted. The proposition that tools served as conveniently available objects for the realization of an "aesthetic" sensibility is supported by the fact that fossils were preferentially placed within the overall form of *handaxes*, as in the West Tofts example. From this standpoint, it is the fact that archaic humans began to exploit accidentally made marks for their own sake that is crucial to this debate.

These insights can be assimilated with the resonance hypothesis by proposing that the early stages of visual processing in visual cortex would have had a predetermining influence on how early mark making arose and developed. The accidental making of straight, repeated lines would have caused these pathways to resonate, stimulating higher areas (concerned with overt awareness), thus creating an indeterminate sensation. Having, in this way, created such lines, the commensurate sense of empathy would then have induced the author to re-enact the experience. Subsequently, having learned how to produce repetitive lines with ease, more intricate geometric patterns could potentially be created by using the initially made lines as a template.

THE SIGNIFICANCE OF SCULPTURED OBJECTS

Yet, there remains the intentionally made iconic artifacts, also from the late Acheulian, for which to account. The contentious Tan Tan figure from Morocco has been provisionally dated to around 400,000 bp (Bednarik 2003b), which is slightly older than the Berekhat Ram find, and may very well constitute the oldest iconic object. As Bednarik (2003b) suggests, the cognitive demands appertaining to the iconicity of these artifacts is relatively simple, as it builds on a visual ambiguity that is rooted in cognitive/perceptual processes found more generally in the animal kingdom. Deacon (1998) regards this as the default mode on which more complex referential systems are constructed, i.e., indexical to abstract symbolic codes. However, there is a difference between simply reacting to these signals and actively engaging in their manipulation for other purposes. This suggests that hominins responsible for these items were intentionally seeking to exploit iconicity (the more rudimentary kind of reference), rather than simply responding to its dictates in stereotyped ways—as is the case for most animals.

These observations can be assimilated with the fact that the Makapansgat cobble, thought to be three million years old, suggests there was a preceding phase of "reflexive" appreciation of naturally occurring objects that happened to resemble such things as faces. The fact that Leakey's (1971: Plate 18) baboon head—a 1.8 million-year-old stone from Olduvai Gorge — is of such antiquity and has been unearthed in the first instance raises the prospect that the capacity for projection may have been quite common at an early period (which lends some support to Harrod's [2003] unsubstantiated claim that certain stones or tools could conceivably be representations of animals or anthropomorphs). However, it seems that it was not until about 400,000 bp when this aptitude came to be applied to a deliberate shaping of naturally occurring objects in order to accentuate the incidental iconicity.

In agreement with Bednarik (2003b), Gombrich (2002) indicates that sculptural artifacts are relatively easy to produce when compared to two-dimensional representations. This is especially so when a particular feature is already implicit in the material and the three-dimensional structure comes freely supplied. In short, the capacity to enhance naturally occurring materials in order to accentuate iconicity, although important as a marker of increasing cognitive sophistication, is not so sophisticated as to make the presumption that the authors were able to indulge in symbol systems, as Bednarik (2003a) proposes, of the more exacting type as defined above. What this does suggest is that the authors were able to take the newly found ability to fabricate symmetrical tools, and, along with the ability to make repetitive marks, transfer these skills to the making of "rudimentary" iconic objects. Crucially, Bednarik (2003b) makes the point that the prominence of symmetry in the

human figure is particularly striking in the Tan Tan object (as well as in the Berekhat Ram find), especially in relation to the central body-line and arms. And, he goes on to emphasise, symmetry is one of the "key factors" in the iconicity of this artifact, which has obvious implications in view of the preceding analysis. Importantly, the Tan Tan figure was found lying only centimetres from the nearest handaxes.

The foregoing suggests that sculptured objects, as iconic representations, should be seen in the broader context of the ability of hominins to produce symmetrical tools and repetitive lines. The generalisation and transference of the skills involved in the production of symmetrical bifaces to other domains, such as mark making and sculptured objects, and the making of shell beads, the latter which have recently been found in Tanzania dating to the Middle Paleolithic layers (Serengeti Genesis Project: www.serengetigenesis.org), constitutes an important indication of the first appearance of true sapient behavior. Moreover, it appears to be too much of a coincidence that the intentional shaping of found items, the increased awareness in the symmetry of bifaces, and mark making should occur at approximately the same time, i.e., beginning about 400,000 bp with the arrival of Homo heidelbergensis whose brain size had now increased from 800-900 cc of Homo erectus to 1100 cc.

We need to bear in mind that the making of marks on stone would have been the least preferred option due to the difficulties posed by a hard surface. So, more pliable, and therefore perishable, materials would have been favoured-implying that mark making probably predates surviving examples by a considerable period. The fact that congruent 3D symmetry (c. 300,000 bp) and broken symmetry (nonsymmetrical but regular shape) seem to appear about the same time (Wynn 2002) as mark making adds weight to the fact that a significant cognitive event was unfolding that served to link these various activities and items together. Wynn (2003) also sees the link between symmetry and mark making in terms of improving cognitive abilities as important. The 400,000 year old wooden spears from Germany discovered by Thieme (1997), which were finely crafted for aerodynamic efficiency, is added evidence to the reality of this hypothesis. It is a hypothesis that predicts that similar tools, artifacts, iconic sculptures, and geometric marks will, at some future date, come to light from the same period. These factors could all be associated with the posited third pathway, which serves to integrate the visuospatial "where/how" with the "what" systems as part of an enlarged parietal cortex in Homo (Bruner 2004).

Despite the existence of iconic artifacts, the preceding deliberations allow us to dispense with the need for symbolic explanations and sufficiently accounts for the appearance of mark making at such an archaic period. In their own terms, deriving from a complex relationship with the world, early marks were not sophisticated in the sense of being part of an elaborate semantic system involving abstract symbols as implied by some authorities (Bednarik 2003a). Yet marks of this persuasion constituted the beginning of an external storage system that could potentially have been be used to hand down information between groups and inter-generationally (Henshilwood and Marean 2003; Hodgson 2000a). They may even, at some point, have come to serve as a *sign* of group affiliation but only in so far as this reflected an associative (indexical) affinity.

CONCLUSION

It can be concluded that the early areas of the visual cortex played a facilitating role in the production of early mark making through several pathways. These pathways will have led to an undefined sense of arousal leading to a raised state of awareness that would have intrigued early humans. Constrained by the way the early visual cortex is structured to process visual information, early mark making would have thus simulated this process by resonating with the mechanisms involved at each stage. In this way, a graphic vocabulary of marks would have arisen, beginning with simple repetitive lines, leading to more complex forms and patterns, as found in the archaeological record. Although not symbolic in the more exacting sense, repetitive marks would have occasioned "meaning" for their authors because they led to a sense of empathy that came to imply order and stability in the face of change. A previously passive appreciation of repetition and symmetry, typical of marks found in relation to some naturally occurring objects (e.g., fossils, crystals, etc.), will have been reflected in a subsequent feeling for the enhanced symmetry of tools as a function of the "what/how" pathway of the brain. An evolutionary newer channel served as a link between the "what" pathway and the visuo-spatial channel that seems to be a function of an enlarged inferior parietal cortex and which, as well as leading to more finely shaped tools, also led to the first intentionally made geometric patterns and sculptured objects. The earliest sculptural artifacts occasioned an elementary form of iconicity, which grew out of a "passive" appreciation of the fortuitous resemblance contained in natural objects, that was facilitated by a growing awareness of symmetry in tools as well as the ability to produce repetitive marks.

REFERENCES

- Appelle, S. 1972. Perception and Discrimination as a Function of Stimulus Orientation: The "Oblique Effect" in Man and Animals. *Psychological Bulletin* 78 (4), pp. 266–278.
- Arnheim, R. 1971. *Visual Thinking*. Berkeley: University of California Press.
- Arnheim, R. 1974. *Art and Visual Perception*. Berkeley: University of California Press.
- Bahn, P. G. and Vertut, J. 1997. *Journey Through The Ice Age*. London: Weidenfeld and Nicolson.
- Balter, M. 2002. From a Modern Human's Brow or Doodling. *Science* 295, pp. 247–248.
- Bando, T. 2000. Spiral Pattern as an Attractor of Human Visual Attention. *Perception - 23rd European Conference on Visual Perception 29*(Suppl.), p. 113.
- Bednarik, R. G. 1984. On the Nature of Psychograms. *The Artefact* 8, pp. 27–33.

- Bednarik, R. G. 1986a. Parietal Finger Markings in Europe and Australia—Further Comments. *Rock Art Research* 3(2), pp. 159–170.
- Bednarik, R. G. 1986b. Parietal Finger Markings in Europe and Austrialia. *Rock Art Research* 3(1), pp. 30–61.
- Bednarik, R. G. 1986c. Parietal Finger Markings in Europe and Australia—Further Comments. *Rock Art Research* 3(2), pp. 159–170.
- Bednarik, R. G. 1990. On Neuropsychology and Shamanism in Rock Art. *Current Anthropology* 31(4), pp. 77–80.
- Bednarik, R. G. 1994 A Taphonomy of Palaeoart. *Antiquity* 68, pp. 68–74.
- Bednarik, R. G. 1995a. Concept-Mediated Marking in the Lower Palaeolithic. *Current Anthropology* 36, pp. 605– 634.
- Bednarik, R. G. 1995b. Metamorphology: in Lieu of Uniformitarianism. Oxford Journal of Archaeology 14(2), pp. 117–22.
- Bednarik. R. G. 2003a. The Earliest Evidence of Palaeoart. *Rock Art Research* 20(2), pp. 3–28.
- Bednarik, R. G. 2003b. A Figurine from the African Acheulian. *Current Anthropology* 44(3) pp. 405–413.
- Bednarik. R. G. (n.d.) Cupules The Oldest Surviving Rock Art. [Go to: http://mc2.vicnet.net.au/home/cognit/ shared_files/cupules.pdf]
- Berkley, M.A., Kitterle, F. and Watkins, D. M. 1975. Grating Visibility as a Function of Orientation and Retinal Eccentricity. *Vision Research* 15, pp. 239–244.
- Berlyne, D. E. 1960. *Conflict, Arousal and Curiosity*. New York: McGraw-Hill.
- Berlyne, D. E. 1971. *Aesthetics and Psychobiology*. New York: Appleton-Century-Crofts.
- Bressloff, P., Cowan, J. D., Golubitsky, M., Thomas, P. J. and Wiener, M. C. 2000. Geometric Visual Hallucinations, Euclidean Symmetry and the Functional Architecture of Striate Cortex. *Philosophical Transactions of the Royal Society of London, B*, 356, pp. 299–330.
- Bruner, E. 2004. Geometric Morphometrics and Paleoneurology: Brain Shape Evolution in the Genus *Homo. Journal of Human Evolution* 47, pp. 279–303.
- Caramazza, A. and Mahon, B. Z. 2003. The Organization of Conceptual Knowledge: The Evidence From Category-Specific Semantic Deficits. *Trends in Cognitive Sciences* 7(8), pp. 354–361.
- Casey, B. J., Tottenham, N., Liston., C., and Durston, S. 2005. Imaging the Developing Brain: What Have We Learned About Cognitive Development? *Trends in Cognitive Sciences* 9(3), pp. 104–110.
- Conkey, M. W. 1980. The Identification of Prehistoric Hunter-Gatherer Aggregation Sites: The Case of Altamira. *Current Anthropology* 21(5), pp. 609–630.
- Cosmides, L. and Tooby, J. 1994. Origins of Domain Specificity: The Evolution of Functional Organization. In L. A. Hirschfeld and S. A. Gelman (eds.), *Mapping the Mind—Domain Specificity in Cognition and Culture*, pp. 85–116. Cambridge: Cambridge University Press.
- Cox. M. 2005. *The Pictorial World of the Child*. Cambridge: Cambridge University Press.

- Davis, W. 1986. The Origins of Image Making. *Current Anthropology* 27(3), pp. 193–202.
- Davis, W. 1992. Beginning the History of Art. *The Journal of Aesthetics and Art Criticis* 5(3), pp. 327–350.
- Davidson, J. and Noble, W. 1989. The Archaeology of Depiction and Language. *Current Anthropology* 30(2), pp. 125–156.
- Deacon, T. 1998. *The Symbolic Species*. Harmondsworth: Penguin.
- Dehaene, S., Izard, V., Pica, P. and Spelke, E. 2006. Core Knowledge of Geometry in an Amazonian Indigene Group. *Science* 311, pp. 381–383.
- Denys, K., Vanduffel, W., Fize, D., Nelissen, K., Peuskens, H., Van Essen, D. and Orban, G. A. 2004. The Processing of Visual Shape in the Cerebral Cortex of Human and Nonhuman Primates: A Functional Magnetic Resonance Imaging Study. *The Journal of Neuroscience* 24(10), pp. 2551–2565
- d'Errico, F., Henshilwood, C. and Nilssen, P. 2001. An Engraved Bone Fragment From c. 70,000-year-old Middle Stone Age Levels at Blombos Cave, South Africa: Implications for the Origin of Symbolism and Language. *Antiquity* 75, pp. 309–318.
- Dronfield, J. 1996. The Vision Thing: Diagnosis of Endogenous Derivation of Abstract Arts. *Current Anthropology* 37(2), pp. 373–389.
- Donald, M. 1991. Origins of the Modern Mind: Three Stages in the Evolution of Culture and Cognition. Cambridge, MA: Harvard University Press.
- Dragoi, V. Turcu, C. M. and Mriganika, S. 2001. Stability of Cortical Responses and the Statistics of Natural Scenes. *Neuron* 32, 1181–1192.
- Edwards. S. W. 2003. Acheulian Evidence. *Rock Art Research* 20(2), pp.109–111.
- Essock, E. A. 1982. Anisotropies of Perceived Contrast and Detection Speed. *Vision Research* 22, pp. 1185–1191.
- Falk, D. 2006. Evolution of the Primate Brain. In W. Henke, H. Rothe and I. Tattersall (eds), *Palaeoanthropology, Primate Evolution and Human Origins* (Vol. 2). New York: Springer-Verlag. [prepublication version available online at: http://www.anthro.fsu.edu/people/faculty/falk/ Handbook_V2.htm].
- Faulstich, P. 1986. Reply to Bednarik Parietal Finger Markings in Europe and Australia – Further Comments. *Rock Art Research* 3(2), pp. 161–162.
- Feliks, J. 1998. The Impact of Fossils on the Development of Visual Representation. *Rock Art Research* 15, pp. 109– 134.
- Feliks, J. 2003. Towards a Comprehensive Paradigm. *Rock Art Research* 20(2), pp. 111–114.
- Furmanski, C. S. and S. A. Engel 2000. An Oblique Effect in Human Primary Visual Cortex. *Nature Neuroscience* 3(6), pp. 535–536.
- Glover, S. 2004. Separate Visual Representations in the Planning and Control System of Action. *Behavioral and Brain Sciences* 27, 3–78.
- Goodale, M. A. and Milner, D. A. Jakobson, A.D., and Carey, D. P. 1991. A Neurological Dissociation Between

Perceiving Objects and Grasping Them. *Nature* 349, pp 154–156.

- Gombrich, E. H. 2002. *The Preference for the Primitive*. London: Phaidon.
- Hamilton-Smith, E. 1986. Reply to Bednarik—Parietal Finger Markings in Europe and Australia—Further Comments. *Rock Art Research* 3(2), pp. 159–160.
- Harrod, J. B. 2003. Lower Palaeolithic Palaeoart, Religion and Protolanguage. *Rock Art Research* 20(2), pp.115– 116.
- Hebb, D. O. 1949. The Organization of Behavior: a Neuropsychological Theory. New York: Wiley.
- Hegdé, J. and Van Essen. D. C. 2000. Selectivity for Complex Shapes in Primate Visual Area V2. *The Journal of Neuroscience* 20. [jNeurosci,2000,0:RC(61)1-6]. (Published online at: http://www.jneurosci.com.org/.cgi/ content/full/3976).
- Helvenston, P. A., and Bahn, P.G. 2003. Testing the "Three Stages of Trance" Model. *Cambridge Archaeological Journal* 13(2), pp. 213–224.
- Henshilwood, C.S., d'Errico., F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G. A. T., Mercier, N., Sealy, J. C., Valladas, H., Watts, I. and Wintle, A. G. 2002. Emergence of Modern Human Behavior: Middle Stone Age Engravings from South Africa. *Science* 295, pp. 1278–1280.
- Henshilwood, C. S. and Marean, C. W. 2003. The Origin of Modern Human Behaviour. *Current Anthropology* 44(5), pp. 627–651.
- Hodgson, D. 2000a. Art, Perception and Information Processing: An Evolutionary Perspective. *Rock Art Research* 17(1), pp. 3–34.
- Hodgson, D. 2000b. Shamanism, Phosphenes, and Early Art: An Alternative Synthesis. *Current Anthropology* 41(5), pp. 866–873.
- Hodgson, D. 2003. Primitives in Palaeoart and the Visual Brain: The Building-Blocks of Representation in Art and Perception. *Rock Art Research* 20(2), pp. 116–117.
- Hodgson. D. 2005. More on Acheulean Tools (Response to "The Large Cutting Tools from the South African Acheulean and the Question of Social Traditions" by Mcnabb, J., Binyon, F. and Hazelwood, L., 2004. Current Anthropology 45(5), pp. 653–677). Current Anthropology 46(4), pp. 647–650.
- Hodgson, D. and Helvenson, P. 2006. The Emergence of the Representation of Animals in Palaeoart: Insights from Evolution and the Cognitive, Limbic, and Visual Systems of the Brain. *Rock Art Research* 23(1), pp. 3–40.
- Holloway, R. 1999. Evolution of the Human Brain. In A. Lock and C. R. Peters (eds.), *Handbook of Human Symbolic Evolution*, pp. 74–125. Oxford: Blackwell.
- Holloway, R. L., Broadfield D. C. and Yuan M. S. 2001. Revisiting Australopithecine Visual Striate Cortex: Newer Data From Chimpanzee and Human Brains Suggest It Could Have Been Reduced During Australopithecine Times. In D. Falk and K. R. Gibson (eds.), *Evolutionary Anatomy of the Primate Cerebral Cortex*, pp. 177–187. Cambridge, MA: Cambridge University Press.
- Hovers, E., Vandermeersch B. and Bar-Yosef, O. 1997. A

Middle Palaeolithic Engraved Artefact from Qafzeh Cave, Israel. *Rock Art Research* 14, pp.79–87.

- Ibbotson, A. and Bryant, P. E. 1976. The Perpendicular Error and the Vertical Effect in Children's Drawing. *Perception* 5, pp. 319–326.
- Joseph, R. 1996. Neuropsychiatry, Neuropsychology, and Clinical Neuroscience: Emotion, Evolution, Cognition, Language, Memory, Brain Damage, and Abnormal Behavior. Baltimore, MD: William & Wilkins.
- Julesz, B. 1981. Figure and Ground Perception in Briefly Presented Isodipole Textures. In M. Kubouy and J. Pomerantz (eds.), *Percpetual Organization*, pp. 27–54. Hillsdale, NJ: Erlbaum
- Klein, R. G. 1995. Anatomy, Behavior, and Modern Human Origins. *Journal of World Prehistory* 9, pp. 167–198.
- Klein, R. G. 2000. Archaeology and the Evolution of Human Behavior. *Evolutionary Anthropology* 9, pp. 17–36.
- Kunst-Wilson, W. R. and Zajonc, R. B. 1980. Affective Discrimination of Stimuli That Cannot Be Recognized. *Science* 207, pp. 557–558.
- Lamme, V. A. F. and Sperreijse, H. 2000. Contextual Modulation in Primary Visual Cortex and Scene Perception. In M. S. Gazzaniga (ed.), *The New Cognitive Neurosciences* (2nd ed.), pp. 279-290. Bradford Books, MIT press: Cambridge, MA.
- Locher, P. J. and Nodine, C. F. 1987. Symmetry Catches the Eye. In J. K. O'Regan and A. Lévy-Schoen (eds.), Eye Movements: From Physiology to Cognition, pp. 353–361. Holland: Elsevier Science Publications.
- Li, W., Piëch, V. and Gilbert C. D. 2004. Perceptual Learning and Top-Down Influences in Primary Visual Cortex. *Nature Neuroscience* 7(June), pp. 651–657.
- Leakey, M. 1971. Olduvai Gorge. Vol. 3. Cambridge: Cambridge University Press.
- McKie, R. 2000. *Ape Man—The Story of Human Evolution*. London: BBC Publications.
- McBrearty, S. and Brooks, A. S. 2000. The Revolution That Wasn't: A New Interpretation of the Origin of Modern Human Behavior. *Journal of Human Evolution* 39(5), pp, 453–563.
- Mithen, 1996. *The Prehistory of Mind*. London: Thames and Hudson.
- Pinker, S. 1997. *How the Mind Works*. Harmondsworth: Penguin.
- Ramachandran, V. S. and Hirstein, W. 1999. The Science of Art: A Neurological Theory of Aesthetic Experience. *Journal of Consciousness Studies* 6(6-7), pp.15–51.
- Ress, D. Backus, B.T. and Heeger, D.J. 2000. Activity in Primary Visual Cortex Predicts Performance in a Visual Detection Task. *Nature Neuroscience* 3(9), pp. 940–945.
- Richards, W. 1971. The Fortification Illusions of Migraines. *Scientific American* 224 (5), pp. 88–96.
- Schoups, A., Vogels R., Qian, N. and Orban, G. 2001. Practising Orientation Identification Improves Orientation Coding in V1 Neurons. *Nature* 412, pp. 549–553.
- Shepard, R. N. 1984. Ecological Constraints on Internal Representation: Resonant Kinematics of Perceiving,

Imaging, Thinking and Dreaming. *Psychological Review* 91(4), pp. 417–447.

- Shepard, R. N. 1990. *Mind Sights. Original Visual Illusions, Ambiguities, and Other Anomalies.* New York: W. H. Freeman.
- Stout, D. 2005. Neural Foundations of Perception and Action. In V. Roux and B. Bril. (eds.), *Stone Knapping*, pp. 273-286. Cambridge: McDonald Institute for Archaeological Research.
- Stout, D., Toth, N., Schick, K., Stout, J., and Hutchins, G. 2000. Stone Tool-Making and Brain Activation: Positron Emission Tomography (PET) Studies. *Journal of Archaeological Science* 27, pp.1215–1223.
- Tanaka, M., Tomonaga, M., and Matsuzawa, T. 2003. Finger Drawing by Infant Chimpanzees (*Pan troglodytes*). Animal Cognition 6, pp. 245–251.
- Thieme H. 1997. Lower Palaeolithic Hunting Spears from Germany. *Nature* 385, pp. 807–820.
- Tooby, J. and Cosmides, L. 1992. The Psychological Foundations of Culture. In J. H. Barkow (ed.), *The Adapted Mind - Evolutionary Psychology and the Generation of Culture*, pp. 19–136. New York: Oxford University Press.
- Tootell, R. B. H., Kadjikhana, K., Vanduffel, A. K. Liu, A. K. Mendola, J. D., Sereno, M. I., and Dale, A. M. 1998. Functional Analysis of Primary Visual Cortex. (V1) in Humans. *Proceedings of the National Academy of Sciences* of the U. S. A. 95, pp. 811–817.
- Turnbull, O.H., Carey, D.P., and McCarthy, R.A. 1997. The Neuropsychology of Object Constancy. *Journal of the International Neuropsychology Society* 3, pp. 288–298.
- Tyler, C.W. 2000. The Human Expression of Symmetry: Art and Neuroscience. [Go to: http://www.ski.org/cwt/CW-Tyler/TylerPDFs/Tyler_SymmetryICUS.pdf]
- Tyler, C. W., Baseler H. A., and Wandell, B. A. 1998. Cortical Regions Responding to Long-Range Symmetry Patterns. [Go to: http://www.ski.org/CWTyler_lab/CW-Tyler/PrePublications/SFN1998/SymmNatureNeuro. html]
- Ungerleider, L.G. and Mishkin, M. 1982. Two Cortical Visual Systems. In D.J. Ingle, M.A. Goodale and R.J.W. Mansfield (eds), *Analysis of Visual Behavior*, pp.549–586. Cambridge, MA: MIT Press.
- Vetter, T., Poggio, T. and Bülthoff, H.H. 1994. The Importance of Symmetry and Virtual Views in Three-Dimensional Object Recognition. *Current Biology* 14(1), pp.18–23.
- White, R. 1989. Visual Thinking in the Ice Age. *Scientific American* 23, pp. 74–81.
- White, R. 1992. Beyond Art: Toward an Understanding of the Origins of Material Representation in Europe. *Annual Review of Anthropology* 21, pp. 297–331.
- Wynn, T. 2002. Archaeology and Cognitive Evolution. *Behavioral and Brain Sciences* 25(3), pp. 389–438.
- Wynn, T. 2003. The Constraint of Minimum Competence. *Rock Art Research* 20(2), pp. 120–121.
- Zeki, S. 1999. *Inner Vision*. Oxford: Oxford University Press.