The Roots of Visual Depiction in Art

The Roots of Visual Depiction in Art:

Neuroarchaeology, Neuroscience and Evolution

By

Derek Hodgson

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For Greta, Mia Rose and Lucinda

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PREFACE

Almost twenty years ago, I began to look at theories that sought to explain the appearance of the relatively naturalistic portrayals of animals during the Upper Palaeolithic in Europe. Despite the fact that the depiction of animals is a quintessentially visual phenomenon, to my surprise, I found almost no reference to recent findings from the neuroscience of vision. Except for a few papers that explored Palaeolithic art from the perspective of perceptual psychology, and probably because, back then, neuroscience was still in its infancy, scant regard was given to the potential insights to be gained from the ever more powerful brain scan techniques. I set out to change this by illustrating how neuroscience could provide novel insights into the reason ancient hunter-gatherers first began to create images of animals. But this could only be achieved by taking into account the deep evolutionary precursors influencing brain function as well as the ethological and environmental context that influenced behaviour. Since those early days, the pace of change in neuroscience has opened up fresh fields of analysis, which are uniquely placed to provide insights into Palaeolithic art. The application of those developments to archaeology became even more imperative given the exciting new discoveries of Palaeolithic art over the past two decades. One of the main barriers to acceptance came, at first, from archaeologists themselves who, understandably, preferred not to stray too far from the material record. However, thanks to a growing interest in cognitive evolution amongst both archaeologists and anthropologists, neuroscientific insights gradually came to be accepted to the extent that a sub-discipline was formed referred to as neuroarchaeology. As a result, neuroscientific research began to be applied to archaeology in areas beyond Palaeolithic art. A further hindrance to acceptance was the fact archaeologists and anthropologists tended to favour "symbolic" interpretations, which meant that archaeological finds continued to be considered from a top-down, higher-order perspective according to socio-cultural criteria. This had the effect of ignoring preconscious bottom-up factors, which neuroscience established has a profound influence on conscious behaviour. I therefore set out to assess whether and to what extent particular aspects of Palaeolithic depictions might be amenable to an analysis from the purview of neuroscience. The contents of this book present the culmination of almost two decades of research that illustrates how an approach stemming from recent neuroscientific discoveries can reap rich rewards for understanding the origins of the earliest figurative art.

Apart from the first part of Chapter Four, entitled “The ‘expedient’ and ‘discerning’ visual brain”, which can be skipped without compromising the essence of the book, the text has been written to appeal to the general reader as much as to those with a specialist interest in the origins of figurate depictions. The more challenging technical concepts have been relegated to the footnotes where those interested can find information regarding underlying principles. The first four chapters provide a grounding for the core of the book, which is to be found in Chapter Five and Six containing the most important insights. The chapters following explore the implications arising therefrom.

CHAPTER ONE

INTRODUCTION

> The dominance of depictions of animals in prehistoric art suggests that the advantages of the animal connection may have driven the development of figurative art… (Shipman 2010, p. 524)

Paradoxes, progress, and definitions

Despite the extraordinary controversy regarding Upper Palaeolithic (UP) art since its discovery in the 19th century, progress towards explaining its provenance has been limited. The lack of progress may be because, except for some very early and contested sculptural artefacts dating to several hundred thousand years ago, fully fledged iconic depictions—in the form of figurines and two-dimensional representations—seem to appear suddenly around 37,000 BP (before present). What is baffling is that many of the first representations were skillfully naturalistic and persisted in virtually the same format for 30,000 years. Having said this, increasing evidence from the archaeological record suggests artistic behavior, which is not in any way figurative, has roots far more ancient than previously surmised. Typical examples consist of ornamental shells and beads as well as ochre used for body colouration, and there is growing evidence for the existence of geometric marks from different parts of the world that predate the depictions of the UP, perhaps dating back 500,000 years. How do these early examples of "art" relate to the much later incarnations? Are they merely isolated occurrences or do they indicate something more fundamental?

A further contentious issue concerns the lack of an accepted definition of art. A problem exacerbated by the fact that, in the west, art has become the preserve of specialist gatekeepers who, based on the prevailing consensus, decide what is to be accepted as such. In fact, today's art is commonly regarded as a luxury associated with increased leisure or greater wealth. Even worse, the skill of making art and a concern for aesthetics are all but derided, making art inscrutable to the wider population. This situation has been muddled further by the fact that, in the modern era, different art practices have become separate areas of concern whereas for early hunter-gatherers such a separation did not exist in that various forms of expression were coextensive. When referring to the art of early hunter-gatherer groups we therefore need to bear in mind that a particular form of artistic activity is invariably linked to other modes of expression as part of a socio-cultural matrix.

The fact that for most of human history art was practised by small scale traditional groups suggests that, in terms of definition, the longer-term needs to be prioritized over the much shorter modern period. In fact, most art was utilized by communities engaged in a hunter-gatherer lifestyle where it was integral to daily life, which is all the more surprising considering the arduous environmental conditions hunter-gatherers had to endure during the Ice Age. The problem of an acceptable definition of art has also been exacerbated by the tendency to ignore how "non-functional" materiality was employed as a means of expression in small pre-literate groups from 42,000 years ago up to the beginning of the historical era; by far the longest period compared to modern western forms of art. In today's terms, art tends to be regarded as non-functional, whereas for pre-modern traditional communities art is taken to be "functional" in the sense that it arguably provided a way of expressing group identity. An approach to understanding art as a behaviourally complex phenomenon, which includes figurative depictions, therefore needs to be based on its origins deriving from at least 42,000 BP up until when this began to change during the early Neolithic period and beyond.

In addition, we need to realise that the art of hunter-gatherers and small scale groups is collective in that all members of a community are involved with various kinds of expression, which are usually experienced co-currently e.g., singing, dancing, visual arts etc. Some activities, however, may occasionally be practised separately by several members within a group. Thus, rather than "art" we would be better served to refer to "arts" when addressing this issue in the present context. A consideration of the role of the arts should therefore be based on when complex multifaceted art first arose around 42,000 years ago. Having said that, we need to take into account the fact that art-like behaviour occurred well before the UP but which was fairly restricted in terms of complexity (Conard, 2008). In order to avoid confusion with the modern usage of the term "art", throughout this book we will often refer to palaeoart, which includes the UP art of Europe, as well as all earlier aspects of rock art and manifestations of artistic behaviour (such as personal ornamentation and geometric motifs) found at many ancient sites globally.

Moreover, since 42,000 years ago—perhaps longer—the arts in one form or another, were practised by all social groups. This is surprising considering the cost in terms of time and effort incurred that could be more profitably directed towards more obvious survival activities. One clue to derivation can be found in the fact that creating and experiencing the arts is inherently pleasurable to the extent that individuals spontaneously engage in such activities without receiving an obvious reward.

A further point needs to be taken into account, aesthetics was not fundamental to hunter-gatherers (Brown and Dissanayake, 2009), which is not to say there was no interest in aesthetics, only that aesthetics remained secondary to the main goal, namely the way material culture helped structure ongoing lifeways (Hodgson and Verpooten, 2014). This is supported by the fact that, although some areas of the brain are dedicated to aesthetic awareness (Ishizu and Zeki, 2011; Brown et al. 2011), no area exists dedicated to a particular art form or the arts in general (Zaidel, 2010).[1]

Understanding the role of art is important because whether it is biological or not is critical in establishing why it prevailed. A number of scholars have taken the biologically adaptive route (see, for example, Dissanayake,1999, 2000; Miller, 2001; Boyd, 2005; Dutton, 2009), though such an approach has been subject to considerable criticism for a number of reasons (see Davies, 2012). An alternative, and potentially more productive, line of enquiry asserts that the arts need to be seen as part of the broader spectrum of material culture that arises from gene-culture co-evolution (Boyd and Richerson, 2005, 2007; Richerson and Boyd, 2001). Accordingly, culture itself is regarded as adaptive but in a special sense—an idea to which we will return throughout this book

One further complication concerns the role of iconic representation, which is often held to be central to the plastic arts. Paradoxically, many small-scale traditional groups up until quite recently did not produce figurative art but relied on elaborate geometric patterns to express their artistic inclinations. Nevertheless, the discovery of figuration represents a crucial boundary in artistic expertise that needs to be contextualized. All the more so, since figurative depiction is intimately associated with art in that it was exploited in many different ways by different groups from around 40,000 years ago onwards. Consequently, a significant portion of this book will be devoted to examining the emergence of iconic depictions as they provide a clue to the first appearance of “complex” artistic behaviour.

The fact today's visual brains are, despite a few caveats, essentially the same as those responsible for the first depictions at the end of the Pleistocene (ending around 12,000 year ago), provides an opportunity to delve into the very minds of our forebears. Stable attributes of this order will allow us to offer some intriguing suggestions as to what art meant to early communities. The first “art” may not only help inform us about those responsible for producing the earliest depictions but also assist in elucidating how early hunter-gatherers related to their world. This is because representational art is intimately associated with how the visual system functions. Indeed, as vision in humans constitutes the dominant sensory modality that operates at an extremely sophisticated level, it may well constitute the overarching influence dictating the course of graphic representation. Closely allied to these issues are the environmental conditions, ecological factors, and perceptual imperatives that nurtured the visual brain. By examining some of those criteria, the possibility arises of identifying the precursors that led to the first representations and how they relate to early human behaviour.

A guiding thread throughout this book concerns the detection of animals, especially as animals were crucial to the survival of palaeo-people during the Ice Age, particularly on hunting forays and during everyday activities when predators needed to be avoided. As a result, the ability to identify animals in challenging environmental situations involving camouflage can be regarded as one of the key factors that led to the human visual system’s substantial capabilities.

This book takes a radically different approach to the human obsession with the arts over the long term, especially the depiction of animals. In pursuing this goal, I hope to persuade you of the relevance of visual neuroscience and neuroarchaeology to understanding the provenance of such inscrutable depictions. An approach to the origins of art from this perspective is viable thanks to the fascinating data deriving from the relatively new science of brain scans, which shows how the visual pathways are affected both by incoming perceptual information and the way this is assimilated across the brain

In order to explore how visual neuroscience and related disciplines can shed light on palaeoart, we apply a “bottom-up” approach beginning with an exploration of the ecological factors that shape the way the early visual cortex processes information in response to evolutionary constraints. Then we move up through the hierarchy of the visual brain towards more elaborate processes until finally reaching the topmost layer where consciousness meets the socio-cultural. Along the way, the relevance of the various findings will be applied to palaeoart ultimately to provide novel insights as to how, and possible why, art was first created. In contrast to symbolic approaches, on which most existing theories are based, this book is grounded on the principles of enactive or embodied cognition that sees human behaviour as closely tied to the material world without much, if any, cognitive mediation in the sense no separation between the subjective and objective is deemed to exist. However, this may be somewhat of a simplification, as how the world is experienced may initially stem from the way it is encoded and held in neural circuits. Thus, cognitive processing is inevitable in that the essentials of embodiment are subject to cognitive reassignment. It is how the world, as perceived, is reconfigured by the higher visual association areas that provides a fascinating new way of approaching the enigma of palaeoart.

Although identifying an object in a graphic image is often taken for granted, it belies a highly complex series of perceptual and cognitive events. In order to understand the means by which the first iconic images were produced, disentangling such complexity is essential. By so doing we will be in a much better position to address issues concerning how the first representational art arose. This is not an easy task as the brain did not evolve to understand itself rather it emerged from the need to deal with ongoing issues of survival and the complexities of social life. As graphic images exist as an extension of the brain, understanding how they first came about becomes even more problematic. In a way, pictures have a foot in both camps, the visual cortex (including the visuo-motor system) and the outer world, which makes graphic images all the more fascinating. It is often claimed, because of its remoteness in time, the reason why palaeo-humans began to create depictions of animals will forever remain a mystery. However, the issue of how and why individuals began producing images of animals is one that transcends archaeology and anthropology as it has implications for understanding the way the brain functions in relation to how “images” are constructed in the cortical systems. It is how the first figurative depictions fit into this broader context that provides a novel twist to this book.

The visual brain on the African savannah

It is generally agreed that the reason the eye evolved five hundred million years ago during the Cambrian explosion was to improve the performance of organisms in detecting prey, thereby promoting successful predation (Parker, 2003; Ingram, 2002).[2] Although the eye eventually became an extremely complex organ, and is one of the "miracles" of the gradual course of evolution, in larger brained mammals the real task of vision takes place in the higher visual brain. Thus, despite the relative sophistication of the eye, we can be sure the visual brain is where real seeing takes place. As the visual areas of the primate brain are responsible for the actual phenomenon of seeing, it is safe to say that, as miracles go, this is an even more astounding evolutionary achievement than the eye itself. This might not seem obvious, as the act of seeing is taken for granted, so that, to the ordinary observer, seeing appears to take place in the eye itself. The fact so many areas of the brain are devoted to visual input suggests otherwise. In fact, the split second it takes to recognise an object belies a complex functional hierarchy whereby the visual image is formed and engages conscious awareness. As the visual faculty evolved over millions of years, and is vital to survival, many of its functions have become unconscious and automatic. The 150-300 ms it takes to recognise an object may give the impression of effortless perception, but the need to detect things in the world quickly and reliably has led to many of the underlying functions becoming automatic. Although this promotes fast reactions to potential threats, it does not describe the underlying neuro-visual processes. By examining research into this issue from the perspective of evolution—especially with regard to form perception—a story unfolds informing us of the very ecological niche in which our early ancestors lived and died.

We should not underestimate the task faced by the visual system during evolution. Think of what is involved in trying to decode the complicated signals that constitute the rich tapestry of the visual array, often referred to as the "blooming, buzzing confusion." In effect, the visual brain has to contend with a torrent of ambiguous information. For example, a particular arrangement of lines, as perceived, can be interpreted in an enormous number of ways. In fact, not even the fastest modern computers come anywhere near the capabilities of the visual system for tackling the problem (Cosmides and Tooby, 1994; Humphreys and Riddoch, 1992), though in the 21st century great strides have been made towards this. How, then, are we able to deal with the confusion emanating from the visual world when most of the perceptual mechanisms operate at a subliminal level?

One of the tricks the visual brain employs is modularity (Foder, 1983), as it not only operates separately to other sensory modalities, but contains subsystems and sub-subsystem that perform different tasks for dealing with raw incoming visual information. This is because it is easier and more efficient for a system to cope with a complex task by having separate specialists at each level rather than having a jack-of-all-trades but master of none. Hence, through modularity the brain is able to divide and conquer thereby simplifying the task in hand. Depending on prevailing circumstances, however, this modularity—especially in humans—may come under the influence of higher cognitive processes (Vetter and Newen, 2014).

In that way, evolution provided ancestral hunter-gatherers eking out an existence on the African savannah from around 300,000 years ago with an exquisitely tuned visual system that helped facilitate survival. How do we know the human visual cortex derived from evolutionary imperatives? One reason is that many of the same or similar visual regions of humans can be found in other primates, such as macaques and chimpanzees (Orban et al. 2004).[3] In addition, vision benefits from its own "intelligence" relatively independent of language, which allows things in the world to be identified and categorised according to inherent processes. From an evolutionary standpoint, it is commonly accepted that visual “intelligence” precedes linguistic understanding because it relies on tacit knowledge gained from long term, as well as ongoing, experience with the world (Hoffman, 1998).

The visual brain was "designed" by evolution in order to cope with the world as efficiently and effectively as possible. Each module is then able to bring to bear its own particular specialisation for the rapid assimilation of incoming data from earlier levels to be transmitted to later stages of the processing hierarchy. Indeed, it has been established that visual areas are not just modular in their different capacities at different layers of processing (horizontally) but also in the pathways that handle the flow of information from one level of this hierarchy to the next (vertically) (Livingstone and Hubel, 1987).

The visual cortex also has separate functional areas and streams that, amongst others things, encode such important attributes as form, movement, and colour. But, the story does not end there—a crucial challenge with which this system has had to deal concerns constancy. Constancy is defined as the ability to attend in predictable ways to information essential to humans as a species that is rendered stable in the face of an ever-changing visual array, thereby enabling signal to be discriminated from noise. As constancy is crucial to our later discussions on art, it is essential to bear this concept in mind.

The visual cortex consists of at least thirty different sub-regions (Orban et al. 2004). In addition, numerous areas partially process visual information throughout the brain, mainly by interfacing with corresponding sensory and associative systems. That complexity demonstrates the importance of vision to hominins even before the appearance of the anatomically modern human brain some 300,000 years ago. Thus, the brain has been shaped by recurring evolutionary events leading to expanded forward visual areas and frontal cortices.

The close-knit relationship between the more obvious attributes of the human visual system and the ancestral environment from which it derives is demonstrated in traits such as stereo vision. This is believed to have originated from the need to perceive insects at close quarters (Julesz, 1995). The decoding of camouflage may also have played a role, as form can be disentangled from distracting cues more efficiently through stereo vision (Allman, 1999). Significantly, front-facing eyes are thought to derive from our role as predators, which confers highly-focused seeing for accurate perception at a distance. One disadvantage of eyes arranged in this manner is that humans become prone to attack from the rear. As social animals, however, the eyes of others group members conveniently serve as a communal lookout in the event of danger.

Surviving on the savannah

Hunter-gatherers from 300,000 thousand years ago originally descended from groups in Africa that had to contend with considerable climatic and environmental challenges during the Pleistocene (Scerri et al. 2018). Late Pleistocene European communities became vulnerable to additional threats, including the vagaries of an extremely cold climate, competing hominins i.e., Neanderthals, starvation, disease, and new predators. Survival depended on the particular faculties with which evolution had endowed humans. Amongst other things, these consist of an upright posture, bipedalism, the ability to sweat, lack of hair, a prodigious opposable thumb, and, of course, a large brain, to some extent fashioned according to the demands of vision (Vyshedskiy, 2014). Ancestral hunter-gatherers, however, remained unaware of the complex, highly tuned visual mechanism that allowed the world to be discerned. They would also have been unaware that this ability existed not to survey the beauty of the world, but rather because it promoted vigilance for the purpose of survival, as evolution functions only at the level of direct action with the world (Milner and Goodale, 1995). Extinction awaited any primate who regarded a plant or animal as a thing of beauty rather than a potential source of food or a threat.

The fact that an indistinct animal could pose a threat or, alternatively, serve as a source of food, meant that enhanced perceptual capacities were essential to promote accurate detection. Identifying an animal in degraded viewing conditions is, however, far from straightforward, as an animal can be seen from a number of directions with the profile changing drastically according to viewing angle. Obviously, learning that an animal is harmful from only one direction, say obliquely, when it might be approaching head-on, is ineffective—hominins would not have survived if this had been the case. Rather, animals are relatively easy to identify from most angles but this begs the question how this skill first came into being.

It transpires that constancy, the ability to recognise an object from a number of different views is, in itself, complex. Not only is it essential to recognise an object from unusual angles but also when size, translation, lighting/shadow, colour, all undergo change. Some of those problems are dealt with in the higher areas of the visual cortex while other more elementary aspects of form are decoded nearer the input end. The early perceptual stages deal with "basic" visual information such as contrast enhancement, edge and contour detection, grouping of common features, texture assimilation, orientation preference etc. In fact, all the way from the retina to the higher brain considerable enhancement of visual information takes place. At the retina, this involves organizing photons as points of contrast by coordinating visual information at the level of the smallest units. However, no image is actually perceived or subjectively experienced at the retina, only a scintillating pattern of spots of light. At the highest level—where a potential approaching big-cat is identified as such—the visual system sees the world in much larger manageable chunks. This is because, from the eye to the later stages, a successive augmentation in the ability to deal with extensive amounts of information occurs; a proclivity achieved through earlier levels in the hierarchy relaying the compiled results to subsequent stages (this process is reflected in the receptive fields, which are smaller in earlier compared to later stages).

Competing with large carnivores for prey was unavoidable during the Ice Age and, accordingly, led to an emotional response in the form of the delivery of massive amounts of adrenaline and corresponding neurotransmitters throughout the nervous system, readying the body for fight or flight. In fact, the emotional brain is alerted well before say a big cat is recognised by the higher visual cortex. How is that possible when the feline may not yet have been consciously identified? The answer is that conscious awareness is "emergent" in that it depends on implicit, preconscious mechanisms (Dehaene et al. 2006; van Vugt et al. 2018). There is, in fact, a pre-conscious route from the early visual centers to the emotional brain (in the limbic system) that is activated before explicit recognition occurs in the inferotemporal cortex and prefrontal areas (at the higher end of the visual cascade). This early warning system, which extends from the initial stages of the visual stream directly to the emotional areas, provides a fast track route that is sensitive to minimal cues for signaling danger (LeDoux, 1994, 2003). As the bodily systems need to be primed for immediate response should explicit recognition confirm what the emotional system suspects, this provides an important and effective safety switch. As it happens, the emotional system seems particularly sensitive to visual cues warning of danger, which has important implications for our discussion on palaeoart in later chapters.

One outcome of those deliberations is that the visual system, although wonderfully adapted for achieving constancy in an ever-changing world, acts as a filter through which incoming information flows. Remember that the visual world "out there" is an infinitely ambiguous commodity, to which the brain has had to adapt in order to extract particular cues critical to survival. This filtering begins at the retina where information, collected by the 101 million retinal cells, converges onto one million fibres of the optic nerve. In order to pass through the filter, information from the retina is extensively edited and condensed with no more than the crucial features allowed through. This means only those aspects of the visual array vital to humans are assimilated by the visual brain. Transmission of the entire visual flux of the world would not only be self-defeating but unnecessary. The visual brain can thereby be regarded as a kind of information cruncher, molded by information that has, over the generations, promoted successful reproduction. It comes as no surprise then, that, in order to pack so much computational expertise into a diminutive brain, the cortex looks like a large walnut, the many folds serving to boost storage-capacity. Yet, despite the millions of neurons and the accompanying billions of interconnections, the visual brain can still be regarded as a kind of filter. Fundamentally, the kind of visual information to which we have become attuned as a species during evolution has determined the information that passes through this filter.

Seeing the same difference

Competition with large carnivores for the same habitat has been implicated as a determining factor in human evolution, especially as we needed to outwit predators through increased intelligence (Brain, 1981; Camarós et al. 2016), which, again, was probably one of the main factors contributing to brain expansion and complexity. Human interaction with animals constitutes an important segment of the hominin evolutionary niche that is reflected in the diverse ways in which various species interact with their habitat by responding to different kinds of visual stimuli. For example, compared to humans, birds and insects are sensitive to a different part of the spectrum (short wavelength), so they see "colors" and patterns in flowers to which we remain oblivious. This is because their nervous systems evolved to be sensitive to such cues as part of a symbiotic relationship with plants. Not only have plants provided nectar for insects as a reward for distributing their pollen but also made sure, by furnishing eye-catching signals, they are easy to spot and locate. Accordingly, insects stood a better chance of passing on their genes. Correspondingly, the flower that attracts the most insects through the best signaling device stands a better chance of spreading its pollen and increasing reproduction. A similar dynamic probably determined the sensory abilities of humans according to the particular environmental factors crucial to survival.

In the case of hominids, evolutionary theory suggests full colour competency originally derived from when primates became daytime rather than night-time foragers. That is, when ripe fruit and berries became a prominent part of the diet rather than mere leaves and insects (Mollon, 1995). Red-green colour blindness illustrates the point, as individuals with this form of blindness have difficultly detecting various kinds of ripe fruit in leaf cover. Indeed, similar to how insects co-evolved a sensitivity to particular wavelengths of light, it is believed plants, especially fruit-bearing trees, shaped human colour sensitivity.

The reward for our early ancestors took the form of sugar and other nutrients in fruit and berries, of which the seeds and pips passed through the digestive tract to be later deposited at a distance as natural manure for later germination. Larger fruit, taking longer to eat, might have been carried to distant locations, where the inedible stones or kernels would have been discarded on the ground. So, we see that the capacity for perceiving colour was honed by the ecological context that specified the spectrum to which we became sensitive. Thus, the environment led to important evolutionary adaptations that stemmed from the relationship between fruit bearing plants and the need for sustenance. In sum, a mesh occurred between the prevailing environmental conditions, on the one hand, and the human visual system on the other, leading to the emergence of particular sensitivities. Another important evolutionary constraint illustrating how adaptive traits formed concerns the human immune system, which evolved from a long-term interaction with bacteria and viruses that culminated in various types of antibodies as part of the human immunological defense system.

Given the way colour vision evolved, is it possible to similarly "backward engineer" the evolutionary precursors for how we came to perceive form? This is perhaps a more fundamental attribute than the ability to see colour, as it would have been almost impossible for a colour blind person to survive on the Serengeti without the ability to see form.[4]

What key evolutionary factors might thereby be responsible for the perception of form? Suppose a big cat is bounding towards one of our ancient ancestors, that individual will have long realised this animal means business and has already taken aversive action by, for example, climbing the nearest tree. But the carnivore would have been stalking for some time, waiting for the right moment to pounce. In which case, an upright posture allows a human look-out—a posture most other primates lack—to peripherally detect movement in the grass. Such an upright stance also comes with the advantage of eyes perched on a tall bony scaffold allowing distant objects to be viewed. The lurking carnivore, however, is aware of this and keeps low to the ground advancing in short, careful, movements. Despite the benefit of camouflage, the predator instinctively knows movement increases the chance of detection in that its upper outline is more apparent against the surrounding vegetation. Movement is such a vital clue to impending danger that peripheral vision is highly sensitive to its occurrence to the extent it has become pre-attentive in orienting the other sensory modalities. The importance of movement is emphasised by the fact a distinct, modular processing stream exists from the retina to the higher visual cortex (known as the magnocellular pathway). Movement thereby provides an initial indication as to the presence of a predator, tagged first by peripheral vision that brings focal vision to bear on the object in question. This is borne out by rods in the retina that specialise in detecting movement—also employed for night vision—that have a longer evolutionary history than the cone system (fovea/colour), which underlines the importance of the perception of movement for survival.[5]

The stalking carnivore, however, might notice such an orienting response and again becomes a rigid non-entity, and the human look-out surmises the disturbance was caused be a sudden breeze or perhaps a small rodent in the undergrowth. It is only when figure and ground become differentiated that the big-cat is unequivocally identified.

The human perceptual "kit-bag" contains further tricks to aid detection. One such trick concerns perceptual priming whereby certain features useful for detecting animals allow anything resembling an animal to be rapidly discerned. The visual system, for example, is particularly adept at detecting contours/edges as well as curved outlines (Gibson, 1933). Those important perceptual "primitives" constitute the bounding contour of an animal, vital for identifying a partially hidden animal. In addition, the preference of the mid-level visual system for good continuation of any disrupted contour means that an outline, which might be attenuated by camouflage, can be discerned. Such capacities derive from the need to achieve constancy in a variety of everyday situations. Interestingly, humans are more able to discern global structure from local features compared to other higher primates (Fagot and Tomonaga, 2001), which derives from an enhanced visual system honed by the need to detect animals in various situations (Vyshedskiy, 2014).

Another scenario where constancy is useful is in subdued lighting. A special mechanism comes into play here, where the recognition system engages in hypotheses-testing by providing options when confronted with uncertain stimuli. Indeed, visual memory may have derived from such a capacity in the sense that the ability to summon images in the "mind's eye" seems to depend on rules employed by the recognition system (Shepard, 1984; Kosslyn et al. 1990; Farah, 2000), thus providing a means to manipulate imagery (Kirby and Kosslyn, 1992). Imagery, however, is prone to fading especially as it lacks updates from immediate sense data, which can give rise to problems with information retrieval and recall. Whether what is experienced visually derives directly from the world or visual memory, this has implications for understanding how artists represent the world.

Many of the perceptual ruses outlined above derive from the need to detect predators or potential prey in "noisy" visual environments. Through camouflage and related strategies, a stalking predator seeks to ensure the environment remains unchanged. In other words, every time a hunter observes what might appear to be an animal, the tracker is duped by the predator into thinking grass, grass, grass, or foliage, foliage, foliage, when, in actual fact, there may well be grass, leopard, grass, or foliage, lion, foliage. This game of hide and seek persisted throughout evolutionary time whereby the human perception/recognition system was shaped by predators targeting hominins. In this way, as much as a predator's beguiling strategies became elaborate, so hominin visual capacities became ever more sophisticated.[6]

The perceptual skills for detecting a partially hidden, degraded, or camouflaged carnivore can be exploited for tracking ruminants and ungulates. Those skills were fundamental to survival because the stalking and capture of animals for consumption provided the necessary protein for brain expansion (Martin, 1983); an organ that requires vast amounts of sustaining energy. As Allman (1999) indicates, larger brains evolved from the need of predators to remain competitive by processing greater amounts of information with increased proficiency. In becoming a top predator, this necessitated that humans engaged in group cooperation, which required a protracted training regime during development (Levy, 1999).

When the visual system becomes emotionally aroused, vigilance towards danger tends to increase, thereby enhancing alertness. That mechanism, however, can become dysfunctional when a traumatic event is experienced, where the original event tends to spontaneously spring to mind (in extremis, referred to as post-traumatic stress disorder). This occurs because unanticipated events lead to a rush of adrenalin that is slow to dissipate, thus helping perception remain primed to any potential danger, which makes sense, as when a carnivore attacks it is likely to loiter with intent—a hunter will be attempting to temporarily remain hidden in the immediate vicinity and big-cats know this. We also need to bear in mind that carnivores and prey were considerably larger and more powerful than modern equivalents leading to sustained levels of arousal. The associated adrenaline surge thereby allows perceptual thresholds to be lowered by facilitating increased sensitivity to any visual cue signaling an animal. An observation that is in line with a conservative evolutionary approach, where it is a safer to respond to an unlikely cue than not because the costs of not responding to a potential cue is much greater than over responding—a better-safe-than-sorry-strategy (Van de Cruys and Wagemans, 2011).

Animals were also important as a source of fuel and clothing—even their bones were exploited for making specialised tools and free-standing shelters. Animals therefore played a crucial role in hunter-gatherer lifeways but it was the predators competing for the same quarry that were especially important.[7] In addition, the tools of hunter-gatherers were mainly used to defend against predators and for the killing and butchery of prey (Bunn, 1981; Potts and Shipman, 1981; Shipman and Rose, 1983, Shipman, 2010). The making and use of tools, however, dates to two to three million years ago, before hominins became proactive hunters, when they were restricted to scavenging carcasses abandoned by large carnivores. The first crude stone tools were therefore utilised to provide access to the nourishing marrow contained in the remains of robust animal bones.

Mayr (2002) suggests that the increase in brain size from Australopithecus to later *Homo* occurred because of migration from a dense tree environment to an open bush savannah. As the savannah was unable to provide enough cover from carnivores, hominins needed to devise strategies to avoid predators. One of the more important strategies centred on better communication through speech, which enhanced the planning and organisation of groups during hunting expeditions (Lombard, 2015). If possible, it is beneficial to consign long-term and reliably persistent properties of the environment to the hard-wired architecture of the brain. This allows information to be stored at the level of genes through genetic assimilation[8] so that the relevant neuronal substrates for encoding important visual stimuli, such as faces and animals, are engaged at an early age. For example, three-year-olds have an uncanny ability to spontaneously classify animals according to basic categories without previous instruction (Gellman, 1990), a topic to which we will return below. Consigning such criteria to genetic markers means each new generation does not have to learn anew, with all that this entails, the uncertainties and dangers suffered by previous generations. Infants therefore have the advantage of being pre-adapted to potential dangers, although, as the child matures, that ability is refined through learning. Related to this, sensitivity to movement—an indicator of potential danger—is thought to be present at birth.

But what has all this got to do with the origins of representational art? In the following chapters, the relevance of the forgoing will become obvious. First, and in order to set the scene as to how art figures in this story, we need to delve further into the inner workings of the visual brain that will reap rich rewards for our later discussions on palaeoart.

Notes

1. The medial orbito-frontal cortex has also been associated with encoding aesthetic criteria (Ishizu and Zeki, 2011)—including an adjacent area—the right orbito-frontal cortex (for the emotional judgments of artworks but also active when observing faces and scenes). Also active when subjects judged abstract artworks as emotionally engaging—especially when linked to “goodness”—is the inferior frontal gyrus (Melcher and Bacci, 2013). Those areas may be interconnected in the sense that the orbito-frontal cortex is associated with person perception and the inferior frontal gyrus with positive affect through connections with the limbic system—where the good and beautiful are associated with empathy, reward and social judgements—suggesting a link to social affiliation. The anterior insula, also associated with aesthetic experience, may be similarly involved in this network (Brown et al. 2011) in that it is also related to empathising (Singer, 2006). As an integrated system for assessing the saliency, value and significance of objects—both social and asocial—for promoting survival, such a network seems to have formed the conduit out of which cultural artefacts could eventually flow (Brown et al. 2011).

2. Parker puts forward "The Light Switch Theory" based on the idea that the first eyes of the Cambrian explosion evolved as a consequence of adaptive pressures to do with the interaction of predators and prey. Ingram holds the view that the eyes of creatures as diverse as flatworms, arthropods, cephalopods, and vertebrates appear to be derived from a prototypical light-sensing organ that was present in the common ancestor of all groups that existed some 550 million years ago.

3. This debate, however, continues to rumble on with those who still hold that human intelligence and consciousness constitutes a step change that makes humans largely independent of the determinants to which the rest of the animal kingdom is

prone. This implies that what makes humans different is still an indefinable quantity but, nevertheless, is probably related to raised awareness associated with enhanced consciousness due to the fact that the higher-order faculties that make humans human are not totally dependent on the lower-order, more modular, structures typical of mammalian brains.

4. Paradoxically, during the Second World War, individuals suffering colour blindness were employed by the Royal Air Force because they were able to discern certain kinds of camouflaged objects more easily than those with normal visual abilities.

5. The cone system is thought to have originally evolved from a mutation deriving from the colour blind rod cells and is therefore much more ancient than cones. Rods were, therefore, tuned to movement before cones came along.

6. In a cave complex at Swartkrans, South Africa, the remains of 130 Australopithecine individuals were found along with those of carnivores and herbivores. It was discovered that the holes in the cranium of a juvenile Australopithecine matched the canines of a leopard from the same cave, suggesting that hominins were hunted just as they themselves were on the road to becoming hunters (Brain, 1981). Brain found that leopards dragged their victims into trees where they were devoured, safe from other predators and scavengers such as hyenas.

7. Particularly important would have been big-cats, hyenas, bears and wolves not forgetting that the large herbivores such as mammoths, bison, and aurochs also posed a real threat.

8. This idea was put forward by Conrad Waddington (1957) who stated that natural selection tends to replace flexible adaptive responses to continuing environmental constraints with genetic predispositions. The consequence of this is that flexible responses during development gradually become more constrained by genetic inheritance, responses that give rise to predispositions towards particular environmental stimuli. Making such responses mandatory provides for a more efficient and less risky behaviour than one that relies on each individual having to learn the relevance of every environmental signal from scratch.

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