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THE BIOLOGICAL FOUNDATIONS OF UPPER PALAEOLITHIC ART: STIMULUS, PERCEPT AND REPRESENTATIONAL IMPERATIVES

Derek Hodgson

Abstract. The representational art of the Upper Palaeolithic continues to be viewed largely from a socio-cultural perspective. This paper takes a radically different approach by investigating graphic mark-making in early humans as a behavioural outcome contingent on a species-specific perceptual predisposition. This is premised on the view that the human perceptual pathways will have been established by the same evolutionary determinants that have shaped the perceptual faculties of other primates. It is the interrelationship between humans, faunas and environment throughout evolutionary time that will be held as the critical factor mediating these systems. Accordingly, because Palaeolithic art, as a visually guided activity, must necessarily engage perceptual mechanisms, it must also be related to the functional constraints appertaining. It is to the nature of these constraints, and the relationship between perceptual factors and palaeoart, that the substance of this paper will be directed.

Introduction

Except for the crude and often ambiguous portrayal of humans, one of the extraordinary facts about Upper Palaeo-lithic art is an almost exclusive preoccupation with the representation of animals (see Deręgowski [1996] for an explanation of the particular difficulties associated with drawing humans leading to their relatively crude and late appearance in rock art). This is all the more remarkable when it is realised that Palaeolithic people would have been living in an environment involving many kinds of stimuli crucial to everyday life, e.g. plants, trees, landmarks etc. Interestingly, animals still tended to be the dominant subject in the Mesolithic and Neolithic periods. Furthermore, animals continued to be a prevalent theme in ethnic and tribal cultures up to the present era and are commonly featured in the art of modern civilisations, both in the East and West. Enduring traits of this order suggest there are factors at work here deriving from deeper causes than cultural affinities. The following deliberations will attempt to investigate the causes for this phenomenon and how the graphic strategies employed might be related to such a long- standing preoccupation. In this respect, the emphasis will be on how the brain has evolved in order to disambiguate the visual world rather than perceptual correlates, the latter of which have been addressed in some depth by, amongst others, Deręgowski (1995) and Halverson (1992a, 1992b).

Relationship between hunting, ritual and perception

Ethology has been defined by Dissanayake (1992: 8) as the study of the behaviour of animals in their natural habitat, which seeks to describe and understand what behaviours characterise a species and how these behaviours have contributed to its adaptedness. In the present context the behaviour of the species we are trying to understand is that of a primate, namely *Homo sapiens sapiens*—more specifically, what led this species to produce the particular depictions found in Upper Palaeolithic art?

There has been much discussion as to what might have led to the portrayal of animals in palaeoart, with little or no real consensus arising as to the precise determinants involved. However, there continues to be an acceptance the depictions may have had, in a general sense, something to do with hunting as part of a wider preoccupation with animals (Bahn and Vertut 1997; Mithen 1988, 1991).

Nevertheless, it is important to emphasise that Palaeoli-thic depiction, as deriving from a long-term concern with animals (in which hunting would have played a role), is not incompatible with the finding that there is often no direct correlation between the species depicted and the diet of Palaeolithic people. Indeed, hunting involves a wide range of activities and behavioural responses embodying a broad knowledge of different factors, e.g. identification of dangerous and benign faunas, migration patterns, species interdependence, dietary needs, methods of stalking etc. Depictive preoccupation with a suite of species at any one time may have reflected a changing psycho-social relation to existing fauna within the domain of natural history brought on by, for example, variation in the distribution or number of given faunas within the context of fluid environmental and climatic conditions (see Mithen 1991; Guthrie 1984). Certainly, animals—as competitors, a source of protein or a threat—would have loomed large in the everyday lives of Palaeolithic people over a considerable period. Moreover, Storr (1972: 139–40) notes that even though, by some accounts, the animals in Palaeolithic art may have been related to different kinds of ritual, this does not detract from the point that ritual itself can *help to increase alertness with regard to animal forms,* thus engendering more efficient identification in the real situation. In other words, the ritual aspects connected to the depiction of animals, when this did eventually arise, may have derived from the original need to focus more acutely on significant fauna as a strategy for promoting survival in a hostile environment.

This suggests the appropriate level of investigation is one that seeks to identify the initial criteria which may have given rise to mythic or cultural perspectives. In this respect, I follow the principle that it is more parsimonious to account for observed phenomena according to a lower level or simpler explanation, when this is sufficient, rather than resort to a higher or more complex level. Accordingly, where a materialistic or functionalist explanation is able to explain particular traits found in palaeoart it will be given precedence over one alluding to meta-narratives.

Evolutionary considerations

In keeping with this principle, evolutionary factors will be held as the primary agency mediating how early humans were able to survive in the world, as well as the expedient by which the perceptual/recognition system became structured. In this respect, a tenet of evolutionary theory is that a creature, in general, follows what is perceived to be its own interests—this is the *ultimate* reason for particular kinds of behaviour; the *immediate* cause, however, may be hunger or thirst. It is through the satisfaction of such motivational drives that, over evolutionary time, an organism (including *Homo*) came to be attuned to certain enduring environmental cues necessary for survival. The visual faculty will have been further refined by those consequential, recurring, evolutionary events that led to its particular morphology and concomitant behavioural outcomes arising therefrom. As a result of this dynamic these cues may have become intrinsic to human perception (Eibl-Eibesfeldt 1989; Fuster 1995; Zeki 1999: 81, 100, 209) suggesting the involvement of an inborn capacity.

An environmental factor particularly significant to Pleistocene hominids, either as a threat or as an important food source (Robinson 1963; Ardrey 1976), would have been fauna—the consumption of which is thought to be *one* of the crucial factors responsible for brain expansion (Martin 1983). Those individuals who were able to perceive and identify such animal forms effectively would have stood more chance of survival and thus pass on the benefits accruing. This process would have been further reinforced by an evolutionary 'arms race' between the stalking and hunting expertise of those species preying on early humans and the human visual system itself. Through these parameters visual modes evolved in a way where the neural substrates increasingly became pre-programmed, allowing for the rapid accommodation of significant environmental cues, thus minimising the need for learning. This is additionally premised on the assumption that the lifetime of any one individual, especially a typical early human, would have been too fleeting for a visual system to learn how to discriminate objects from the prodigious complexity of the ambient optical array

What, therefore, are the precise characteristics of the determining cues arising from this scenario and how might they have evolved and affected archaic humans?

Arousal, perceptual sensitisation, Fixed Action Patterns and sign-stimuli

Sensitivity to significant environmental cues (such as animal forms) in hunter-gatherers would have been contingent on levels of hunger, mediated by a drive-reduction, approach-avoidance scenario (Rosen 1954; Vernon 1971: 204). The reticular activating, cortex (Vernon 1971: 192–4), autonomic and limbic systems (Ramachandran and Hirstein 1999) would have also been involved in this feedback loop, thus increasing attention and focal vision.

Moreover, as Oakley (1983) has argued, this kind of 'preparedness' derives from a species' history, in that exposure of individuals to particular kinds of significant associations over long periods leads to this information being instantiated genetically, so it can be transmitted across generations. At this level, sensitivity to animal forms can be related to implicit perceptual processes where the system is pre-primed to respond to such shapes as the occasion arises (Thorpe et al. 1996; VanRullen and Thorpe 2001). With regard to Palaeolithic art, Feliks (1998: 116) has emphasised the value of this factor in relation to 'race cryptomnesia' which may be connected to pre-primed perceptual co-ordinates._

Preparedness can be linked to a mechanism discovered by Tinbergen and Lorenz concerning Fixed Action Patterns (FAPs) and sign-stimuli (Lorenz and Tinbergen 1938; Tinbergen and Perdeck 1950; Tinbergen 1951; Veen et al. 2000). FAPs are thought to be in-built and lead to stereotyped patterns of behaviour which have developed in a species throughout its evolutionary history due to adaptation (Lea 1984). Additionally, each species has its own typical repertoire as distinctive as inter-species physical characteristics (Hinde 1982). Sign-stimuli (key stimuli), or releasers, are those environmental cues significant to an organism's survival which are sufficient to trigger FAPs. Furthermore, as Hinde has stated, the most effective stimulus is not necessarily the one resembling the natural stimulus as artificial stimuli, which exaggerate obvious aspects of the natural releaser (and are a kind of caricature of the original known as a supernormal stimuli) generally evoke a more intense response (together with Gombrich [1977, 1978], Ramachandran and Hirstein [1999], and Bedaux [1996] have likewise alluded to the relevance of supernormal stimuli in the context of art).

Alcock (1998: 142, 149) has defined this process as stimulus filtering whereby a nervous system, through natural selection, responds selectively by extracting relevant information from the sensory barrage while, at the same time, ignoring a great many other things. Here, organisms 'zero in' on biologically significant items and environmental events as cues associated with predators or prey. Different species are thought to have different neural mechanisms that perform these tasks as necessary. Alcock (1998: 152–3) cites *the human perception of contour and edge as a predetermined capacity of the visual system which 'encourages' the detection of critical and specific stimuli such as a partly hidden animal.* This phenomenon, he concludes, can occur at higher levels and is a universal attribute underlying perception (Alcock 1998: 173). In relation to this observation, some investigators have verified that a variety of animals are able to recognise, with little or no training, certain objects drawn in outline on flat surfaces (Cabe 1980: 324–5).

FAPs and sign-stimuli are a phenomenon Gombrich (1977: 87; 1978: 5–7; 1982: 285–6) has alluded to in the context of art regarding certain perceptual features to which humans may be pre-programmed. Surprisingly he did not relate this to Palaeolithic depiction with any real conviction, and only then in respect to his own more favoured, but much criticised, projection hypothesis.

In fact, Gombrich (1982) subsequently went so far as to admit that we do not acquire knowledge about such things as teeth and claws in the same way as we learn a language and these attributes will be more easily recognised than, for example, the features of aircraft. In this respect, he cites how cultures exploit ease of recognition in the making of such objects as threatening masks. Similarly, he went on to emphasise, human survival depended on the recognition of meaningful features of objects that were to be avoided and which we are predisposed to scan the world for. Consequently, the greater the biological relevance of a feature, the greater the ease of recognition—however remote the objective resemblance, and this is true of animals as it is of humans; e.g. the use of decoy ducks and angler's deceptive lures as enticements. Moreover, Gombrich further stipulated, illusionary resemblance to things is a device commonly found in the natural world; such as a moth that looks like a leaf, or an insect that looks like a twig. Such cues, I would venture to add, are employed in these various scenarios as a means of encouraging the unwary into 'thinking' something is there when, in fact, it is not—so that such devices might (a) tempt a creature to respond inappropriately to something that simulates the real thing, (b) act as camouflage to beguile a potential predator, or (c) assist a predator to remain concealed. In this regard, Gombrich went out of his way to stress how recognising an image can be a complex process involving both inborn and acquired faculties. He also underlined the necessity of a pre-determined, natural starting-point without which it would be impossible to acquire a skill. This, he concluded, presupposes a hierarchy of responses, some of which are easily triggered, whereas it is necessary to be conditioned to discover others.

I refer to Gombrich's comments at some length because, although he defended the priority of top-down processing through hypothesis testing in perception as set down by Gregory (1966), he was, nevertheless, ready to admit some necessary pre-ordained mechanisms on which higher-order processes are predicated. Coincidentally, this accords with Peirce's [1897, 1903] theory of semiotics that posits a hierarchy of meaning where increasingly complex and sophisticated layers of associative contingency are mediated by subordinate levels, i.e., from iconic, to indexical, to symbolic. This is supported by recent observations of an evolutionary trend in perceptual aptitude in primates from baboons through to humans (Fagot and Tomonaga 1998; Fagot et al. 1999). Bednarik (1986a: 44) anticipates this view by stating that humanness is a 'function of the degree of competence in perceiving an image' that may be complemented in the ability of other primates etc., also to perceive an image.

The question arises, how might this be related to early hominids and, given the importance of animals, what specific features of these would have been relevant to the continuing survival of humans? This question will be addressed after considering evidence relating to a possible predisposition for the human perception of animal forms.

Evidence for innate human perception of living things

It has been demonstrated that even some 'lower' organisms, such as cuttlefish and chicks, have the ability to benefit from experience so as to respond more accurately to innately constrained determinants (Wells 1958; Hailman 1969). So, although more pronounced in humans, a certain amount of flexibility similarly exists in animals that helps enhance perception. The opportunity to modify innate factors in *Homo sapiens*, however, is more apparent due to a top-down cognitive overlay (Weiskrantz 1982): a flexibility, or plasticity, which is realised optimally as a species-specific adaptive specialisation (Plotkin 1997: 60; Öhman 1986). As Nash (1970: 299) has commented, these innate determinants may be so overlaid as to be indiscernible. Interestingly, as Tinbergen (1972: 217) noted, notwithstanding proximate factors, what is *likely* to reveal an ancient 'deep structure' in humans constitutes whatever is inter- and intra-culturally least variable.

It is obvious that important enduring cues should have an automatic dimension, as they would be triggered at an earlier age with greater efficacy as opposed to having to be learned anew for each individual or generation, hence providing better survival outcomes. Appositely, this has been given some credence by computer simulation of evolutionary theory, which demonstrated that when an environment is stable there is selective pressure for learned abilities to become increasingly innate (Pinker 1994: 242).

Controversially, Coss (1985: 273) has argued, the mammalian nervous system can retain information about former habitats for thousands of generations (see also Fuster 1995: 9, 10). Fundamentally, Warrington and others (Warrington and Shallice 1984; Warrington and McCarthy 1987; Farah et al. 1991; Moss et al. 1997) have found evidence for cognitive categories of living and non-living things, whereby the former are defined in terms of their *underlying visual attributes*, in contrast to the latter, which depend more on functional specifications (see also Laiacona and Capitani 2001). Crucially, it has been discovered there is a precise area of the brain, part of the left inferotemporal cortex, which is specifically devoted to the naming of animals from pictures at *basic category level* (Damasio et al. 1996). The same researchers found adjacent cortical areas for face and tools, indicating the brain does, indeed, apparently have *specific modules for the identification of certain objects.* Hence, it can be surmised that, as modules, these brain areas will have been contingent upon long-standing evolutionary processes during the Pleistocene when *Homo* was still a hunter-gatherer. It is therefore reasonable to assume these areas will have been forged by dint of a common, iterative, perceptual history that endured over evolutionary time.

The question of the relationship of neurophysiological areas to the actual processes of perception, although not yet proved, is supported by increasing evidence that lower to higher-order systems indicate a hierarchical scenario of progressively complex feature extraction culminating in such modules (Tanaka 1996; Oram and Perrett 1994; Logothetis and Sheinberg 1996). Furthermore, as Zeki (1993) has pointed out, theoretical debates about perception need to be founded on the neurophysiology of the visual system rather than the other way round. Accordingly, perceptual insights might furnish suggestions as to how the visual brain functions but it is the neurophysiology that provides the ultimate confirmation.

Correspondingly, Logothetis et al. (1995: 553) have pro-posed the perception of biological forms may be contingent upon specialised neural populations. Coss (1985: 256), similarly, has established that two facing eyes, relating to the identification of predators, is an in-built neural substrate of humans, which affords the recognition of the Gestalt that in turn relates to releasing mechanisms such as flight or fight. Tanaka (1996: 126) has successfully located actual neurones in the inferotemporal cortex responsible for this effect while noting, at the same time, that different and particular groups of cells respond to simplified, critical features of objects distilled from both animal and plant forms (1996: 111).

Oram and Perrett (1994: 962) have proposed that be-ha-vioural decisions about visual attributes can be made at an early stage of processing as required—as earlier stages of the visual cortex are thought to be more innately determined than later areas (Farah 2000) this has obvious implications in the present context. Indeed, Kosslyn et al. (1990) have demonstrated how this can operate through *antecedent trigger mechanisms in response to ambiguous or degraded incoming visual stimuli and how higher-order feedback helps to improve signal- to-noise ratio, as need arises, using imagery as a kind of back-up system* (lower level is defined as V1 through to V4 in the visual cortex). So, the early visual system seems to home in on those simple, distinctive visual cues typical of an object, and once these are tagged the recognition data-base fleshes out the image as a fully-experienced, conscious image. By tagging incoming visual information in this way the visual system might be helping to limit the number of matches necessary to categorise an object at higher levels (Lowe 1987).

The alerting and early processing of essential visual data in the visual pathway can be related to the orienting response: a general, pre-attentive mechanism in the midbrain which reacts to novel stimuli (Öhman 1986). In relation to this scenario, Pinker (1997: 386) notes that monkeys born in captivity scream when they first see a snake—or even a length of plastic tubing crudely resembling this type of creature.

More generally, Atran (1990) and Berlin et al. (1973) have found the way humans spontaneously categorise biological objects at genus level is the same cross-culturally. Furthermore, Gelman (1990) established that children, as young as three years of age, can make distinctions between the animate and inanimate according to certain essential features without prior learning. Quinn et al. (1993) found three- to four-month-old infants were capable of discriminating cats, dogs and birds based solely on perceptual characteristics.

With reference to classical and instrumental conditioning, the possible existence of an innate component comes from the fact that little inducement is required to build up phobias to certain animals or dangerous places, with no evidence for previous conditioning to these stimuli (Seligman 1972). Öhman et al. (1975a, 1975b), for example, paired slides of snakes and spiders with strong electric shock and quickly established conditioned emotional responses but not with slides of flowers, houses or berries. In addition, such responses were formed after only one trial, and a *degraded stimulus* was found to be sufficient to trigger a phobic response to animals via subcortical, thalamic-amygdaloid connections, in contrast to other kinds of stimuli (Öhman and Soares 1993: 130). Öhman (1986: 128–9) also makes the point that we fear animals because predation pressure has been a primary force shaping our gene pool throughout mammalian evolution. As reactions must be rapid and automatically recruited with little inhibitory influence, the response tends to have an unconscious component to minimal input with resistance to extinction (Öhman and Olofsson 1975).

Related to the foregoing, Rorschach (1942) has noted that animals were the object category most often perceived in the Rorschach Test. In addition, individuals who suffer from Bonnet's syndrome (Schultz and Melzack 1991), a condition where peripheral vision degenerates, commonly experience hallucinations involving cartoon-like animals. These observations are particularly relevant to Ice Age art as many of the depictions are situated, and were therefore executed, in dimly lit caves thus, to some extent, simulating Bonnet's syndrome. Likewise, Siegal (1980) cites that, in over five hundred reported drug-induced hallucinations, half included animals and humans, mostly in the form of caricatures.

Significantly, peripheral (non-foveal) vision has been found to be particularly sensitive to flicker or movement and can be experienced pre-attentively, serving to direct attention to the initiating cause (Wilman 1966: 92; Vernon 1971: 139; Thorpe et al. 1999). As peripherally perceived motion would have been an important indicator of danger, issuing, in the main, from a potential predator, this may have evolved as a capacity specifically designed for the immediate bringing to attention of any life-threatening forms.

Finally, and more generally, Allman (1999) and others (e.g. Mollon 1995: 133) have suggested that colour vision and binocularity in hominids may have developed as a means of disambiguating different types of fruit in the forest leaf canopy and, similarly, front-facing eyes evolved as a consequence of our role as predators.

If such basic perceptual correlates can be put down to reciprocal interactions between early *Homo* and environment, we can be assured other aspects of perception, as carried out by the visual brain, are likewise conditioned by concomitant influences. Equally, most psychologists (e.g. Pinker 1997) would agree that visual illusions (including depictions) are effective because they manipulate the normal rules by which the visual system has evolved in order for humans to survive in the world.

In summary, it seems the brain has in-built capacities that allow for early and rapid responses to particularly important stimuli crucial for survival. The stimulus-bound properties of the perceptual response patterns elicited constituted the foundation on which more sophisticated recognition processes could be built. In this way, *Homo sapiens* became biologically predisposed to certain kinds of learning that have led to particular brain modules speciali-sing for objects such as 'natural things'.

Relationship of sign-stimuli to the use of contour and line in Palaeolithic depiction

A number of specific attributes of Palaeolithic art suggest that it is related to sign-stimuli: (a) distillation of form to its essential ingredients leading to depiction of salient parts, (b) universality, (c) repetition of particular graphic devices, e.g. use of outline, typical view etc., (d) stereotypi-cality, (e) inflexibility of content over a prolonged period, (e) exaggeration of fundamental cues, (e) a cartoon-like quality.

I direct readers to Halverson (1992b), as well as Kenne-dy and Silver (1974), for confirmation and detailed account of outline as a universal or innate capacity for the indication of figure and ground, boundary and silhouette in human perception (see also Jones and Hagen 1980: 220–1).

Not only did Halverson demonstrate how *simple outlines in the depiction of animal forms take preference over fill-in detail* (citing Kennedy 1974) *but also how this device encapsulates distinguishing features important for the identification of particular classes of animal* (Halverson 1992b: 394). Mithen (1998), Clottes (1989) and Deręgow-ski et al. (1996: 426) have made a similar point. Halverson, as well as Davis (1986: 194), noted that incomplete line representations, such as the mammoths from Rouffignac cave (indicating the prominent features of the back and head), are a common characteristic—especially of early Upper Palaeolithic art (e.g. Aurignacian).

Furthermore, as Mithen (1988: 309), in referring to the ethnographic literature, indicates, the hunter pays particular attention to diagnostic characteristics of an animal, such as the antlers or horns, making the point that the twisted perspective of Palaeolithic art allows identification of such significant anatomical traits as a homologue to perceptual imperatives for distinguishing game in situ.

Halverson sees such abbreviated outlines as necessary for feature detection, but also argues that the perception of these features seems to be built into the visual apparatus (Halverson 1992b: 400) via the matching of a mental norm image (1992b: 398) honed through previous experience of humans as a species (see also Deręgowski and McGeorge 1998a: 45). Halverson concludes:

> Artistic conventions seem pretty clearly to be secondary, culture-specific developments *based on primary, species-specific biological structures and processes depictively reflected in outline drawings.* The universality of such drawings argues against any notion of primary conventionalism. On the whole, the issue seems to be something of a red herring, at least in the case of basic line drawings, and is generally rejected by psychologists (Halverson 1992b: 400, my emphasis).

Paradoxically, although Halverson admits outline pictures are ultimately rooted in neurophysiological and evolutionary history, he is at a loss to see how this can confer any biological advantage (1992b: 402–3). The above analysis, relating to key stimuli, can help resolve this question, by showing how the graphic elements typical of Ice Age art are a product of the same visual mechanism employed to disambiguate significant objects embedded in the optical array.

Moreover, and notwithstanding occasions where uneven surfaces were exploited to enhance 3-D effects, palaeoartists often went to great lengths to create smooth areas on which outlines could be drawn (Clottes 1998: 117; Davis 1986 [comment on Davis by R. White, p. 208]). In any event, the use of uneven surfaces can be interpreted as subsidiary to the main concern with contour—correspondingly, as in perception, textural effects that suggest depth can also be seen as supplementary to the outline contour (Biederman and Ju 1988) as the outline itself has been found to provide cues from which solid form can be extracted (Koenderink 1984). Importantly, lines, as edges and corners, remain detectable in peripheral vision while information that is dependant on detail is lost (Hochberg 1978; Zusne 1970). This may be because in moving away from the fovea to the peripheral areas of the retina we are travelling back to an earlier evolutionary stage that once proved useful in visual processing and on which later, more sophisticated, stages were built.

In short, outlines appear to sufficiently encode 3-D forms leading to shape constancy and thus ease of recognition, which explains why they are employed in palaeoart as an effective means of representing solid 3-D forms in a 2-D format. Deręgowski (e.g. Deręgowski and McGeorge 1998a, 1998b; Deręgowski et al. 1996) has shown how this can be economically achieved by way of the typical outline based upon particular geometric factors—applicable both to the real world and in degraded depictions as found in palaeoart. This is defined by Deręgowski as 'a line of curvature change on the surface of a solid which connects points of greatest change of curvature' that is, 'a globally defined curve connecting points of maximum curvature whose principal direction corresponds to the minimum curvature' (Deręgowski and McGeorge 1998b).

Halverson and Deręgowski's disagreement on these issues rests on what exactly constitutes a typical outline (see Deręgowski 1995). Deręgowski's position is set out in detail in Deręgowski et al. (1996), which demonstrates how geometric properties of an object, as defined, can, in the first instance, determine how the perceptual system is able to take advantage of such affordances as contained in the flux of the optic array. Halverson's position, however, seems to rely more on how salient parts, or distinguishing characteristics, determine the ability to recognise an already familiar object from different viewpoints. Deręgowski's claim seems to be the stronger. Not only is it based upon more objective criteria, but it also demonstrates how the perceptual system can take advantage of geometric parameters that determine the appropriate plane of typicality, which will subsequently facilitate the expeditious recognition of unfamiliar objects. In contrast to Deręgowski, Halverson, it would seem, does not address this particular question.

In this respect, abbreviated outline contours (or typical outline) can be considered as an analogue of sign-stimuli that were originally moulded by selective pressures. These will have been determined, at the outset, by the geometric factors identified by Deręgowski. It may be because the human visual system evolved to take advantage of such invariances that they served as the basis for sign-stimuli from which the recognition of animal forms could be derived. The distinctive line of an animal—tusks, antlers, horns, dorsal features etc., were, therefore, probably the defining stimuli, or 'releasers', critical for the survival of early hominids that acted as a perceptual 'shorthand', as the most efficient and quickest means of identifying fauna. As the typical outline of most quadrupeds is determined by the direction of the spinal column (following the line of maximum curvature along the direction of minimum curvature), it is along this part of an animal where most of the defining features are likely to be found.

This has recently been confirmed by Fritz (1999) who established that, almost without exception, the sequence of actions used to depict quadrupeds in Magdalenian mobiliary art reflected cues for optimum identification which involved first, the head and antlers/horns, then the neck-dorsal line (1999: 196–7)—a procedure which was found to be the same cross-culturally during the period. Fundamentally, Fritz and Tosello (2000) verify the same sequence of actions in the depiction of the 'confrontational' Chauvet rhinoceroses—some 15 000 years in advance of Magdaleni-an depictions!

It logically follows that abbreviated outlines should figure so prominently in Aurignacian art, and form the template for later Palaeolithic art, considering their enduring importance for the continuity of early humans. FAPs then become the approach-avoidance behaviour in terms of fight or flight, motivated by a drive reduction mechanism (Hull 1943; Grossman 1967), such as hunger, as part of a coping response (McEwen 1995) that induces sensitivity to particular sign-stimuli releasers.

Such forms were not, as Davis (1986) suggests, discovered by the accidental attribution of iconic status to artificially produced lines or natural objects, but rather by recourse to the hominid perceptual system that had previously become attuned to stimulus-bound features through evolutionary imperatives, i.e. *those constraints which had determined the functional outcome of the hominid perceptual system also became important as a trigger for the motifs to be found in Upper Palaeolithic 'art' through a sharing and exploitation of the same visual mechanisms.* Hence, in a situation that might involve the identification of ambiguous perceptual stimuli (often involving camouflage and partially hidden forms), a distinct advantage would accrue in being primed to respond to certain distinguishing traits (e.g. Kosslyn et al.'s 1990 trigger mechanism in the early visual buffer).

Bednarik (1986b: 165) has similarly argued that the objects dominating the visual experience of early hominids would have been those evoking the most profound desires and fears, such as large mammals, and these may have been portrayed in palaeoart because they would have been 'imprinted' more strongly than others in a taxonomic visual system.

In support of this proposition, Mithen (1988: 311) and Bahn and Vertut (1997: 137) have noted there is often an *exaggeration of certain features* in this 'art'—this accords with the concept of the supernormal stimuli, as a means of verifying and authenticating fundamental adaptive cues, and as a way of assessing the tolerance levels involved in triggering recognition systems.

Exaggeration and supernormal stimuli

These observations are consistent with cognitive data that has explored the significance of exaggeration in human perception. Evidence using caricatures in outline drawings and photographs of 3-D objects suggest that exaggerated features, deriving from an average or prototype of a particular category, may be more recognisable than the true or veridical image (Rhodes et al. 1987; Benson and Perrett 1991). Fundamentally, when subjects were presented with such exaggerated images they were frequently able to recognise the identity of the image more quickly, often with increased accuracy. The caricature advantage, as it is known, is taken as support for the existence of a prototype of basic object categories being stored in memory. Rhodes et al. (1987) suggested the matching of the caricature to stored veridical templates might lead to a greater relative activation of the target object compared to non-target distractors. Caricaturing could, therefore, provide a shortcut in the search process because exaggeration of features would make it easier to access the actual features of the target object. Interestingly, Rhodes et al. (1987: 110) suggest that we are adept at recognising caricatures because the minimum information afforded is accentuated in the sense that it is super-normal.

These insights can be related to the cartoon-like quality of Ice Age art, as one of the defining characteristics of cartoons is the identification and exaggeration of prominent features, equivalent to a supernormal stimulus. So the object, although degraded, becomes easier to recognise than a more natural representation (see also Ramachandran and Hirstein 1999).

The prevalence of sign-stimuli

This is an explanation which sufficiently accounts for the predominance of fauna, outline boundaries, abbreviated lines, exaggeration, attempted realism and the cartoon-like quality of many of the depictions in Palaeolithic art. The proclivity to depict animals over such a prolonged period can, ultimately, be accounted for by an interaction of several complementary factors: first, the influence of sign-stimuli as mediated by evolutionary dictates and instantiated in neural networks; second, the preoccupation of humans with fauna on a day-to-day basis and inter-generationally; third, the fact that animals either posed a threat or were a source of sustenance.

As sign-stimuli had probably been a crucial determinant in the survival of hominids during the whole of the Pleistocene, if not longer, this puts into proportion the twenty thousand-year preoccupation of Ice Age artists with a graphic analogue derived from this template. Accordingly, other relevant environmental stimuli, except perhaps for the female form, e.g. ‘Venus’ figurines (to which much of the foregoing could equally be applied), probably did not figure prominently in Ice Age art because there were fewer interacting elements involved. However, as Deręgowski (1996) has shown, although the perception of fellow humans would also have been important for survival, the drawing of people involves particular kinds of difficulties concerning the identification of the typical contour (to do with ambiguities peculiar to the human form) that does not apply to the depiction of animals.

Conclusion

This account, although presenting evidence for certain capacities of the human visual pathways that can be compared with similar capacities in animals, also illustrates the particular kinds of events peculiar to human evolutionary history that led to certain features becoming ‘hard-wired’. Hence, in-built processes enabled a repertoire of response strategies to be facilitated with a minimum of learning to critical cues essential for survival when these were encountered in the environment. It was due to this predisposition that the primary motif of this art (and subsequent art) came to be vested in fauna and the related, typical, graphic characteristics emerged.

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I am indebted to various parties for their help towards compiling this paper, including anonymous reviewers of *RAR* and others who have offered suggestions as to how the paper could be improved. I would particularly like to thank the Haddon Library at the University of Cambridge for the provision of documents, and Greta Desforges-Hodgson for her assistance with references.

Derek Hodgson
2 Belle Vue Street
York, North Yorks YO10 5AY
England, U.K.
E-mail: *dhgson@email.com*

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RAR 20-618

RAR COMMENTS

The roots of art and the European Upper Palaeolithic

By JOHN BRADSHAW

In his ambitious synthesis, Hodgson, I believe, fails to look beyond the confines of Upper Palaeolithic Ice-Age Europe, and overemphasises ‘graphic mark-making in early humans as a behavioural outcome contingent on a *species-specific perceptual predisposition*’ (my italics). He also overempha-sises the role of *biological* forms, of *animal* rather than *human* content, and of *outline* drawings. There are traditions of representational art in Australia which are almost as old and certainly as complex and as developed as those of Old Europe—and the exquisitely detailed ‘Bradshaw’ paintings (Gwion) of the Kimberley stand in antithesis to Hodgson’s thesis; they are infilled (not line), invariably of human subject matter, and they involve action. A preoccupation with animal referents in the European Upper Palaeo-lithic could be merely a local phenomenon. I also feel that he gives undue emphasis in his argument to innate releasing mechanisms, and ‘supernormal’ sign stimuli; all art is necessarily a selective emphasis, by some form of caricature, of a chosen aspect or feature. Indeed, all the aspects of Palaeolithic art which Hodgson claims specifically relate to sign stimuli (distillation, universality, repetition, stereotypicality, inflexibility of content, exaggeration of fundamental cues, cartoon-like quality) are merely the most economical and effective ways of characterising objects—*any* objects.

‘The greater the biological relevance of a feature, the greater the ease of recognition …’, ‘these features will be more easily recognised than, for example, the features of aircraft’, says Hodgson. Again I would dispute a fundamental primacy of biological form in perception. We learn from the agnosias (the acquired loss of a pre-existing capacity, through injury, to recognise certain classes of object) that there is nothing magical, or fundamentally different in kind, between ‘natural’ and ‘artificial’ objects, even though in certain instances of category-specific perceptual loss there may be selective preservation, or loss, of one or other broad category. (There may be selective impairment of the capacity to recognise only fruit, or vegetables, or tools, or large—but not small or vice versa—items of furniture—indeed, of almost any class or category you can think of.) A native tracker may be exquisitely tuned to the spoor of his quarry, and an aircraft or train spotter to some equally minuscule mechanical nuance of his or her obsession. We surely possess a far more general, than Hodgson allows, feature-sensitive analysing system which is not restricted to prey, or even biological objects or forms.

Again, I feel Hodgson overemphasises the capacity of ‘lower’ organisms ‘such as cuttlefish and chicks … to *respond more accurately to innately-constrained determinants*’ (my italics). Pigeons can be trained to perform a quality-control sort on a production-line of light-globes, some of which may be defective, even faster and more accurately than we can ourselves; and chimps readily learn to recognise and differentially respond to arrays of arbitrary symbols and icons on a keyboard.

To turn the question on its head: the problem may not be so much a question as to why or how early art arose, but, rather, why it was *not* present even *earlier* in our evolutionary trajectory. The existence of manuports—objects found and apparently preserved by individuals as far back as the *Lower* Palaeolithic Acheulian—speaks to an early aesthetic sense, or at least a realisation of a perceptual or imaginal potential in an inanimate natural object such as a pebble. So maybe the problem in our primate ancestors, just as with language, lay in the *production or realisation*, rather than in the reception, conception or understanding. Bonobos cannot paint, but they can comprehend line drawings; they cannot speak, but they sure can understand complex spoken commands. Indeed, I am unconvinced that there are any specific *perceptual* adaptations which greatly distinguish us from our hominid ancestors, or even the apes; rather, I believe it is a matter of limitations of motor realisa-tion, and that, contrary to Hodgson, it is also at the motor rather than just at the perceptual end that we should seek to explain the emergence of early forms of art.

Two other minor points. We should be wary of invoking 'specific brain modules for the identification of certain objects'. Modularity theory is rightly nowadays giving way to a view of the brain as a collection of systems or circuits, whose functioning boundaries are fluid, depending upon the particular constraints of the moment, rather than in terms of enclosed, encapsulated 'expert systems'. Indeed, recent imaging studies relating to recognition of tools invoke *frontal*, rather than *temporal,* regions—a far more likely scenario, in fact, given the action aspect of tool use. Secondly, I dispute that 'drawing people involves particular kinds of difficulties concerning the identification of the typical contour … that does not apply to the depiction of animals'. Again, in other regions of the World, we see parietal art of the human form ranging from static or dynamic stick-figure representations to extremely dynamic Gwion paintings, fully infilled, in the Australian Kimberley region.

The above comments notwithstanding, I applaud Hodgson's provocative, scholarly and ambitious synthesis.

John Bradshaw PhD DSc
Emeritus Professor (Neuropsychology)
Department of Psychology
School of Psychology, Psychiatry & Psychological Medicine
Monash University
Victoria 3800
Australia
E-mail: *j.l.bradshaw@med.monash.edu.au*

RAR 20-619

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The archaeologists' mind and the Palaeolithic eye

By J. B. DEREGOWSKI

The paper examines evidence of biological foundations of Upper Palaeolithic art. Unfortunately the relevant data are, as the extensive bibliography shows, through no fault of the author, very unevenly spread. Practically all the data concern perception of pictures; few of them concern the vector responsible for the creation of depictions. There are in the literature of the subject numerous speculations as to the nature of the vector, but these in essence are vague guesses (were the pictures made as magical devices? Were they records of past events? Etc.). The author rightly ignores these. The present commentary attempts to accentuate some of the issues touched upon by the author.

The author mentions, in passing, Coss's (1985) observations on the significance of the eyes. These observations can be expatiated on by noting that human beings are not the sole species which respond strongly to cues provided by the eyes. Hinton (1974) has shown how eyespots on the wings of certain moths protect them from predators. Bern and Herzog (1994) have carried out an experiment in which garter snakes were confronted with models which either had or did not have eye-spots. The snakes struck at the former significantly more frequently than against the latter. Thus the same device (the eye-spots) evokes either fear or aggressiveness depending on the species; but both testify to its cogency. (For relevant evidence obtained from children see Dziurawiec and Deręgowski [2002]). It is important to note that this effect derives not from real eyes but from their depictions. The eye-spots, it appears, easily break the barrier between the depictions and the depicted.

Depictions of eyes in pictures much more recent than the Upper Palaeolithic provide further relevant evidence. Pictures of certain schools disclose the perceptual conflict between eyes and typical contours. They do so by means of 'distorted' portraits which combine profiles or near-profile views of heads with about frontal views of the eyes. Elaborate Spanish monastic portraits of the eleventh century show that such pictures are not mere *lapsi penicilli.* Works of Picasso and other modern painters confirm this, as do the depictions of Mormos, the Aborigine ghosts that dance on the graves in Australia. (See Deręgowski [1984] for illustrations of this phenomenon.)

This suggests the following questions: why are the eyes generally ignored by the Upper Palaeolithic artists? Is it possible that those artists shied from the difficulty of depicting two non-coplanar elements: the typical contour of the animals' body and its eyes?

There is some evidence that portrayals may be affected not only by purely perceptual factors but also by the ergonomic factor of the ease of their execution. Namibian and Saharan rock art includes depictions of giraffes with their spines vertical but in their shape identical with neighbouring depictions of normally orientated giraffes. The 'vertical' giraffes have been called ‘sitting giraffes’. It is an odd term since giraffes are not known to ‘beg’ in a doggish manner. However, young European children required to draw giraffe-like models tend to draw ‘sitting giraffes’, most probably because they found it easier to draw thus (Deręgowski and Berger 1997). Therefore the problem is probably solved by reference to ergonomics.

The purpose of the visual system is to make sense of the stimulation which impinges upon it. It pursues this end to the extent of seeing portrayals of objects in patterns created by pure chance such as inkblots. Inkblots present the extreme of ambiguity but whatever the stimulus the information reaching the system is to some extent ambiguous and leads to various perceptual hypotheses as to its significance (Gregory 1974a). Bednarik’s (1986c) brief comment is apposite here.

The flux of information arriving at the eye from a depiction is not treated differently from the flux derived from any other source, although it does contain certain elements which, if attended to, may enable the observer to conclude that he is looking at a depiction and if attended to exclusively may make him fail to see the picture. Since the same system is concerned with perception of objects and depicted objects there is, as the author shows, a considerable body of evidence about its *modus operandi.*

Since one can see a depiction in an inkblot it is obviously easy to make a picture, provided that it is accepted that in that picture the observer will see whatever he wills. This is not however, generally, the artist’s intention. The artist wants the observer to see a specific object, and although the perceptual rules as to the features of the model which need to be depicted can be stated, it is not immediately apprehensible how the very notion of depiction comes about.

The author refers approvingly to Davis’s (1986) assertion about the origin of image making. This, Davis maintains, may be regarded as a step in the continuing evolution of the visual system. If this were so then one would expect all sane members of all human groups to be equally capable of drawing, at least in the manner of the draughtsman of the Upper Palaeolithic. This is, however, not so, as Fortes’ observations on the Tallensi show (Fortes 1940, 1981; see also Deręgowski 1978).

Therefore ‘biological foundations’ of picture making appear to be less sound than ‘biological foundations’ of picture perception. Perhaps all that is needed is the author’s elucidation.

Professor J. B. Deręgowski
Department of Psychology
University of Aberdeen
Kings College
Old Aberdeen
Scotland
E-mail: *psy022@abdn.ac.uk*

RAR 20-620

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Is an appeal to biological factors sufficient to explain Palaeolithic rock art?

By THOMAS HEYD

Palaeolithic rock art calls for explanation which appeals to other factors than the merely biological, in so far as palaeoart is the result of an *intentional* and *cultural* process in ways that digestion or gestation, for example, are not. The process is intentional because rock art typically does not usually issue from doodling or as a by-product of some other activity: much, if not most, rock art displays images that reflect a production process which evinces the artistic skill and aesthetic judgement that went into their creation. The process that generates rock art is cultural because it involves skills in creation and in the appreciation of representations that require inter-generational development, group interaction, and transmission to bring about cross-fertilisation, sophistication and learning of productive techniques.

Derek Hodgson’s paper provides a useful account of likely factors that may *underlie* a general tendency among Palaeolithic artists (at least in Europe) toward the depiction of animals rather than many other objects, such as plants, landmarks etc. His paper does *not*, however, constitute a case against accounts of palaeoart that directly focus on ‘mythic of cultural perspectives’ or that allude to ‘meta-narratives,’ as he suggests. At least with respect to palaeoart, it likely is not ‘sufficient’ to ‘account for the phenomena according to a lower level or simpler explanation’. Several factors speak against giving ‘precedence’ to a biological focus in explanation of Palaeolithic rock art, as Hodgson proposes.

As noted by Hodgson, palaeoart *can* be seen as posing problems from a purely ethological point of view, for example, in so far as the relative frequencies of species represented in extant marks on rock do not seem to match the hypothesised frequency of species in dietary habits of Palaeolithic people. But, in so far as we are dealing with representations that reflect the intentional creation of sophisticated aesthetic values, they also always pose problems of *meaning*.

We can ask what particular images meant to the individuals that made them, and how they were interpreted from within the culture to which those people belonged. Certainly explanations of meaningful phenomena should also take into account functional constraints and evolutionary predispositions, but such constraints and predispositions only constitute the *boundaries* within which explanation must be located. Rather, when interpreting *meaningful* marks, the way such phenomena are (or were) understood *by their makers* is of central importance.

To my knowledge no one has provided us a reason to doubt that the individuals who made Palaeolithic rock art were fully human, capable of language and of conscious analysis, at least up to the level needed for the invention, intentional change, and manufacture, of tools; for the maintenance of communal life; and for the development of inter-personal skills adaptive to their respective natural and social environments. *Homo sapiens sapiens* who lived 10 000 to 30 000 years ago are *much closer to us* than to the distant hominid forebears who, through evolutionary selection, first acquired the basic perceptual equipment and strategies that we still exhibit today.

Consequently, we should not suppose that explanations, primarily appealing to the conditions that brought about basic perceptual capacities and readied our hominid forebears for specific perceptual saliencies, can be especially helpful in the explanation of sophisticated artistic manifestations such as we find at sites such as Lascaux or Chauvet, as Hodgson proposes. Rather, given that we have reason to suppose that the palaeoartists in question are relatively close to us in cognitive and perceptual capacities, it may be quite appropriate to extend *back to palaeoart* contemporary assumptions about motivations for making and for evaluating pictorial representations, at least up to a point, unless there *are* substantial reasons against it.

In other words, it is inappropriate to explain Palaeolithic rock art phenomena by relying on reductionist accounts stemming from biology for the same reason that it is inappropriate to rely on such accounts in the explanation of contemporary phenomena such as modern painting, classical music, or architectural styles. Both the more recent and the less recent phenomena call for another kind of analysis precisely because they are, respectively, embedded in complex, socio-cultural patterns.

The explanation of cultural facts, such as marks on rock, naturally requires consideration of biological preconditions, such as the capacity to distinguish salient features in the visual field but, for their proper, full explanation, further considerations, relating to their cultural *Sitz im Leben*, are relevant. This is not the place to give more than an hint of what this means, but we may consider comparative studies focussed on the role of visual marks in the landscape for orientation and as historical reminders; the evolution of art styles within small societies; and their use as insignia.

It has long been convenient to treat certain artistic manifestations as 'primitive', since the label, indicating that something belongs to the 'first' or 'initial' phase of humanity, would appear to point to a starting place for the presumed evolutionary *ascent* of human beings to *our own* contemporary artistic achievements. As of late, however, the discovery of the sophistication of cultural systems in societies formerly treated as 'primitive' belies this approach, and possibly even makes it out to be a form of cultural supremacism.

So, I conclude that Hodgson's account of biological foundations of Palaeolithic art should be considered for what it is, namely a useful description of biological factors that may be contributory to the prevalence of motifs featuring fauna over those featuring flora and landmarks in palaeoart manifestations. It should not be assumed, however, that, as such, that sort of account could provide a *sufficient* explanation of the choice of motifs in palaeoart.

Qua intentional, *prima facie* meaningful, manifestations of human beings who, by all likelihood, were living in cultural interdependence with many earlier generations of artistically and aesthetically skilled people, Palaeolithic rock art images call for an account of their *cultural* foundations, evolution and contexts. No appeal to parsimony can justify neglect of these latter dimensions which, naturally, supervene on the more basic, biological.[1]

Dr Thomas Heyd
Department of Philosophy
University of Victoria
Victoria, British Columbia
V8W 3P4, Canada
E-mail: *heydt@uvic.ca*

RAR 20-621

Cognitive linguistics, and thinking about animals, cross-culturally

By ALICE B. KEHOE

Cognitive linguistics

Hodgson cites research in cognitive psychology and neuroscience, to which he could add work in cognitive linguistics such as that by George Lakoff and his collaborators (Lakoff 1987; Lakoff and Johnson 1999 and citations therein, a topically organised syllabus).

Lakoff and Johnson open their 1999 book with three statements: 'The mind is inherently embodied' (that is, the 'metaphors we live by', to use their 1980 title, primarily come from physical experiences such as 'feeling down' from being unable to stand up when ill); 'thought is mostly unconscious', and 'Abstract concepts are largely metaphorical' (Lakoff and Johnson 1999: 3). They continue, 'human reason is a form of animal reason, ... inextricably tied to our bodies and the peculiarities of our brains. ... [O]ur bodies, brains, and interactions with our environment provide the mostly unconscious basis for our everyday metaphysics, that is, our sense of what is real' (Lakoff and Johnson 1999: 17). Clearly, these scholars offer consilience, recommended by Stephen Jay Gould in his final magnum opus as the 'principal tactic' for the historical sciences (Gould 2002: 104).

One important derivation from cognitive linguistics is that scientists, no less than other humans, speak in embodied metaphors (Lakoff and Johnson 1999: 111). Because this tends to go unnoticed, metaphors may unduly affect observation and analyses. I have noticed this particularly in use of conflict and aggression terms where the organisms, or even inanimate conceptualisations such as molecules, cannot be premised to be conscious agents: e.g., a *New York Times* report discussing a book called *Sperm wars: the science of sex* (Yoon 1996). That sperm are said to 'compete', that fruit fly copulation can be a 'deceptively cooperative act', not only is silly, it is pernicious. Indo-European linguist Benveniste found that in these languages, 'the normal state

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[1] For helpful suggestions I am indebted to John Clegg and Brian Butterworth.

was war, to which peace ... intervenes as a sometimes accidental and often temporary solution' (Benveniste 1973: 299), exactly the position expounded by Augustine of Hippo (St Augustine) and thus authoritative for millions of Christians (Marrin 1971: 57; Kehoe 1988, 1998).

Thinking about animals, cross-culturally

At the seminal 1986 World Archaeological Congress in Southampton, several sessions discussed thinking about animals cross-culturally, to broaden archaeologists' inferences from art and faunal remains. These were published in the One World Archaeology series by Unwin Hyman, London: Ingold (1988); Clutton-Brock (1988); Morphy (1989); Willis (1990). Tim Ingold, who has devoted his professional career to human-animaI interaction studies, subsequently published another edited volume (Gibson and Ingold 1993) and a collection of his own essays (2000) that includes several quite pertinent to Hodgson's discussion. Steve Baker presented a literary critics view in *Picturing the beast* (1993). A sensitive recent ethnography, *Grateful prey: Rock Cree human-animal relationships* (Brightmau 1993), with Tanner's (1979) *Bringing home animals* and Frank Speck's classic *Naskapi,* present Northern Algonkian understandings of animals in their lives; Brightman's book has a good bibliography. T. Kehoe (1990) is a discussion of Palaeolithic art approached from the study of American Plains bison pounds. A consensus from these researches is the saliency of animals in human social relationships, not only as focus of subsistence tasks, but iconically. Writing this note at the end of the annual deer hunting season in Wisconsin, I am reminded how persistent these icons can be—in spite of chronic wasting disease (a cervid version of mad cow disease) having been identified this year in Wisconsin white-tails, schools and businesses closed and thousands of men congregated in cabins with buddies, reinforcing a camaraderie more valued than celebrating American Thanksgiving that week, maybe it is hard-wired in their brains.

Professor Alice B. Kehoe
3014 N. Shepard Avenue
Milwaukee, WI 53211-3436
U.S.A.

RAR 20-622

Commentary on D. Hodgson's 'imperatives'

By STEVEN J. WALLER

D. Hodgson proposes the theory that Upper Palaeolithic art, which is dominated by faunal themes, was the manifestation of 'hard-wired', 'pre-programmed' templates that evolved in the brains of early hominids. He emphasises the universality of these visual 'Fixed Action Patterns'.

Hodgson's theory, while intriguing, is not provable since, even if there were some scientific way to document a catalogue of exactly what these supposed brain image templates look like, there would be no way to prove that these templates were the reason the artists produced the art. The theory does not stand up well to logic since the evidence of different species of animals drawn on different continents by the same species of humans is inconsistent with the theory that humans have built-in images in their brains that evolved over millions of years. If Hodgson were correct, we would expect these brain templates to be manifest in a consistent pattern, no matter where humans migrated. If the human brain has built-in templates of 'tusks, antlers, horns' itching to be creatively expressed, then why were not elephants, bison and deer depicted in the early rock art of Australia? The humans that migrated to Australia should, according to Hodgson, have had the same urges as European humans to depict the 'common, iterative, perceptual history that endured over evolutionary time'. If it is argued that the artist would have had to see for him- or herself the real animals as environmental cues, or 'sign-stimuli', in order to 'trigger' the Fixed Action Patterns, then the argument becomes little more than 'They drew what they saw', which is no more helpful than the 'Art for art's sake' argument.

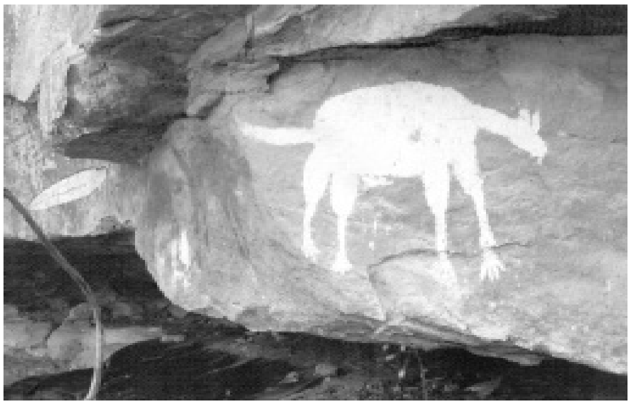

Figure 1. *Marsupial depiction in the rock art of the Laura region, Cape York Peninsula, Australia.*

Furthermore, Hodgson's stance is that the artists were only capable of depicting the repertoire of images that already existed in the human brain as a result of millions of years of evolution. The credibility of this stance is ruled out by the corpus of Australian art that features species of animals that are unique to that continent, such as marsupials, to which humans were not exposed during their evolutionary process (Fig. 1). It is not reasonable to expect in-born kangaroo or wombat templates that would explain their presence in rock art. Even though the dates of human migration to Australia are uncertain (see e.g. Spooner 1998), there would simply not have been enough time for evolutionary processes to result in such specific templates. Thus, since the Australian kangaroo images cannot and need not be explained away by genetically attained brain templates, then neither would the European art need such a template explanation.

Hodgson's attempt to explain the unusual locations of European cave art is weak. He relates the dimly lit caves to

Bonnet's syndrome of peripheral vision hallucinations. This is a far cry from explaining why some artists went so deeply into the caves and only decorated certain chambers. If mere darkness was the requirement to elicit the template images, then the art could have been executed simply at night on readily available surfaces, rather than being performed in remote recesses the artists risked their lives to attain.

I also take exception to Hodgson's presumption that Palaeolithic art was a 'visually guided activity', upon which he bases his approach. Although rock art does itself consist of visual traces, there is accumulating evidence pointing to acoustics as an important influence; see Dauvois (1996), Hedges (1993), Ouzman (2001), Reznikoff and Dauvois (1988), Steinbring (1992) and Waller (1993, 2000). Perhaps what Hodgson is interpreting as a set of hard-wired templates is actually something more along the lines of the filtering process that occurs in the brain as part of converting sensory stimuli into meaningful cognitive perception. Hearing certain sounds can precipitate certain visual images (Hosler 1994)—so that, for example as I have found, percussive echoes may evoke images of either hoofed animals or kangaroos ('boomers', as the big ones are called). Such cross-modality synaesthesia is discussed by Houston and Taube (2000), who emphasise that

> [v]arious sectors of the brain process such visual and auditory flags through the formulation and testing of cognitive hypotheses (Gregory 1997: 10): that is from an infinity of possibilities, what exactly is the object being seen, what is the nature of the sound being heard? Such mind-generated assertions about reality are 'representations' that do more than simply show pictures: they also annex background information that gives meaning to the perceived object or sound (Gregory 1997: 8).

I would encourage Hodgson to pursue his interesting ideas more along these lines, rather through the notion of rigid hard-wired images.

Dr Steven J. Waller
5381 Wellesley Street
La Mesa, CA 91942
U.S.A.
E-mail: *wallersj@yahoo.com*

RAR 20-623

REPLY

Perception, recognition, evolution and palaeoart: interactive hierarchies and reciprocal correspondences

By DEREK HODGSON

The rather controversial nature of this paper had led me to anticipate a somewhat adverse response. The largely favourable and informative comments are therefore encouraging. I will address issues raised according to main subject categories as indicated by different headings.

Innate factors, culture and neurophysiology as compatible traits

One of the main criticisms raised by Heyd and Waller concerns an over-dependence on innate factors as a sufficient explanation for the derivation of Palaeolithic art. In citing Plotkin, and referring to the term hard-wired in quotation marks, I make the point that this concept has to be seen in the light of the past developmental histories appertaining to a species. In other words, learning is biased by previous selection events that now exert their influence through a genetic shaping of those structures of the brain that subserve learning and memory. Therefore, learning, as well as flexibility, is just as much an adaptively defined trait as any other aspect of human behaviour or physiology. In this sense, determinism does not equal inflexibility. Accordingly, individuals are primed to acquire certain kinds of knowledge effectively and rapidly that will become manifest as they interact with the proximate environment.

In this regard, Bradshaw seems to have misinterpreted the point about 'lower' organisms. The emphasis here was on an organism's ability to learn from experience despite innate constraints. As Bradshaw himself shows, the fact that 'lower' organisms can learn to a considerable degree demonstrates learning from experience is not a preserve of humans but is a widespread phenomenon. This is not to say that innate criteria do not continue to constrain behaviour as conditioning experiments with animals have shown limits to this capacity according to species-specific traits.

Relating this more directly to the present context, there is strong evidence to suppose that a hierarchy of response strategies underlie recognition. LeDoux (1994) has found that the subcortical thalamus to amygdala pathway of humans and animals responds similarly to potentially threatening stimuli, especially predators. Consequently, there are two routes for reacting to a dangerous event—one cortical, the other subcortical, with the latter being the quickest and most immediate. In fact, the subcortical pathway seems to provide only a *crude* perception of the external world whereas the cortical route furnishes a more detailed enhanced representation. This system may trigger an emotional response to a stimulus before conscious recognition ensues, hence allowing fight or flight mechanisms to be readily tuned—this is because not responding to a stimulus involves more costs than responding. The brain may therefore simply need to store primitive cues of basic information that can be verified by a delayed-functioning higher recognition system. Thus, the two systems operate in unison to provide a seamless conscious experience. Interestingly, LeDoux has found that these kinds of emotional driven memories are difficult (if not impossible) to erase. A consequence of this is that the alerting system produces a generalised attentional bias to focus on threatening stimuli that tend to persist when activated, as dangers do not strike in isolation, then disappear, but rather tend to linger (Öhman and Soares 1998). This often leads to a further entrenchment of anxiety/emotional arousal and a concomitant increased motivation to seek further threats of the same order (a mechanism known as adaptive conservatism).

This has important consequences because presumably, during the Lower to Upper Palaeolithic, hominids would constantly have been prone to aversive experiences involving predators. As a result, this would have led to similar anxiety-provoking emotional memories. Interestingly, as Clottes (1998) notes, compared to the Magdalenian, animals depicted during the Aurignacian tend to be the more threatening variety. Of course, animals will have been significant on a number of counts, not just as predators or a source of food, but also for clothing, tools, fuel etc. From this perspective, cultural factors and biological considerations need not be mutually exclusive. Thus, proximate and distal components will have come together in emotionally adapted contingencies to imbue animals with virtues beyond obvious utilitarian needs that *eventually* led to culturally mediated myths and rituals. Within modern hunter-gatherer groups these factors have been found to impinge on social relations (Charles 2000) and, as some of the references cited by Kehoe demonstrate, the link between culture and the materialistic resources afforded by animals can be extremely fluid. Mundkur (1988), in particular, has shown how various cult practices such as shamanism, which are often centred on animals, can be interpreted as outlets for fear and anxiety concerning fauna. As a 'lower level' explanation this is sufficient to answer the question of why animals were universally portrayed, as well as accounting for the profile view. This does not, however, exclude 'higher order' cultural factors that sought to interpret these contingencies in manifold ways.

Picture perception or picture production— the meeting of comprehension and action

Both Deręgowski and Bradshaw allege that the theory is more about picture perception than picture production. Similarly, Van Sommers (1984) has shown how important ergonomics can be for drawing outcomes, particularly if the author is left or right handed. Nonetheless, Van Sommers makes the point that perceptual imperatives continue to be essential. Relating this to palaeoart it is interesting that, although great control and draughtsmanship are obvious, the authors persisted with the profile view and outline contour for prolonged periods. Interestingly, there seems to be no privileged direction, left or right, towards which a represented animal is disposed. Assuming most of the authors were right-handed (Bahn and Vertut 1997), one would expect a bias for left-facing animals (see Van Sommers 1984). In fact, one would expect this bias to have been even more accentuated in caves—the light having to come from the left in order for the shadow of the hand not to obscure the drawing surface. The lack of preference in direction can be addressed in what is known as 'virtual views'. In other words, the perceptual system seems to depend on a mechanism that is not yet fully understood, for flipping immediately from the right to left-facing profile view without the difficulties incurred for accessing unusual views, i.e. intermediary views (Johnson 2001). In this case, perceptual factors seem to overrule ergonomics. Although this does not discount the fact that in other instances, such as the drawing of an unfamiliar or more complex object (such as the human figure), the planning procedures involved might take precedence over perceptual criteria. Set against this is the fact that it has been established, despite infants having the motor dexterity to produce appropriate marks for the realisation of certain objects, this is not achievable before a certain age due to perceptual constraints (Phillips et al. 1978). Similarly, it has been established children will draw the more difficult aspect of a presented object even if this is not immediately available (Deręgowski and McGeorge 1998b). So, although motor functioning is obviously important in depictive endeavours, perceptual factors can be equally if not more decisive.

The related problem raised by Bradshaw, that the components of sign-stimuli are merely the most effective way of characterising any object in depiction, fails to take into account that an arguably more effective means of representing animals might have been to portray off-axis views. As unusual views are virtually non-existent in palaeoart this is as informative as those aspects that were actually included. Interestingly, the typical view seems to have constituted the default mode of representation in many subsequent manifestations of art. This can be related to long-term visual memory that is mediated by lower visual correlates. For example, Blanz et al. (1999) have established that when individuals visualise objects in the 'mind's eye' this tends to be in the form of the typical profile view. This is because mental images are subject to internal storage and processing economy but still need to be highly diagnostic. Moreover, Ramachandran and Hirstein (1999) have shown how the notion of sign-stimuli is related to graphic expertise through the concept of 'peak shift', which is a perceptual response whereby aspects of a stimulus can be made more potent through distillation and exaggeration of decisive behaviourally defined vectors.

The origins of art

Bradshaw rightly believes an aesthetic sense goes back as far as the Acheulian. The question arises, however, why do we not find 2-D representational forms before the Aurignacian? Given that geometric lines of various types (such as the recently confirmed Blombos artefacts, c. 77 000 BP; Henshilwood et al. 2002) crop up in the archaeological record at increasingly earlier dates, this may have been due to a gradual evolution of abstract geometric forms that will have eventually come to suggest animal or human outlines from which later representational art developed (Hodgson 2000a; 2000b). The ability to produce graphic primitives will also have led to a perfection of fine motor skills essential to the realisation of 2-D representations. The fact that the Chauvet depictions are so sophisticated, and predate much of what was once thought to be the simpler representations of the same period and later, suggests that representational art probably has even more ancient roots. The case I make regarding sign-stimuli predicts that any new discoveries of *representational* art that predate Chauvet will be mainly of animals, in a similar format as stipulated, or, to a lesser extent and in cruder terms, humans.

Deręgowski appears to have misconstrued my comment on Davis's notion about the origin of representational depiction. I was, in fact, critical of Davis's position by stating that such forms *were not*, as Davis (1986) suggests, discovered by the accidental attribution of iconic status to artificially produced lines or natural objects. Rather it was the fact because early humans were particularly tuned to certain evolutionary important forms that, through projection (as in inkblots), it was virtually inevitable these forms would be seen in a matrix of previously assembled lines, even if this matrix was initially produced by accident. The Tallensi, who had never drawn before, first produced such a matrix in which certain crude animal-like forms in profile seem to be evident (Deręgowski 1989: Fig. 9). In any case, as 'passive' comprehension in perception-recognition usually precedes pro-active exploitation of this cognitive facility, hominids had probably been engaged in projecting their main fears and desires onto various naturally occurring configurations long before actual iconic depictions were produced.

Modules for natural categories—an enduring factor?

Bradshaw's observation, that tools invoke frontal regions of the brain, is consistent with the temporal regions also being implicated as this reflects a passive/active dynamic for engagement with this type of object. Interestingly, Solso (2001) shows how the right temporal region and frontal areas of the brain are activated when an artist actively engages in the drawing of a seen object. This is supported by the finding that the prefrontal and posterior association cortices are functionally linked (Hasegawa and Miyashita 2002). Although Bradshaw is correct in stating that brain modules for classes of objects have become more 'fuzzy' nowadays, nevertheless there is still strong evidence for category specificity (e.g. Caramazza and Shelton 1998) even if this is based upon distributed neural networks. I note, however, Bradshaw does not dispute the crucial claim as to the reality of broad category divisions.

The related point, pertaining to there being no special difference between natural and artificial objects in terms of processing time, has been addressed by studies indicating that individuals can, in fact, take *longer* to disambiguate natural things, such as animals compared to artificial objects. This is because the former are composed of curved lines that share more similar features than carpentered objects (Levin et al. 2001; see Gazzaniga et al. 1998: 187–92 for a review), which may be a consequence of animal forms co-evolving with visual systems in order to promote dissimulation.

Evocation of salient features, prototypes and subordinate recognition systems in palaeoart

As to the sensitivity to the nuances of objects raised by Bradshaw, there is increasing evidence that this is a function of the right hemisphere. Warrington (Davidoff and Warrington 1999) and others (e.g. Humphreys and Quinlan 1987) believe this hemisphere acts as a back-up system or optional resource to the left hemisphere for the perception of occluded, degraded or exemplar information. In other words, the left hemisphere (encoding for the usual view) is thought to provide a quick, efficient route for immediate recognition and interfacing with language systems—whereas the right helps to flesh out the template with details for ascertaining the subordinate level category should this be required.

So, the tendency towards refinement of visual information seems to begin with primitive cues at lower subcortical levels (see LeDoux above). Then, to the clarification of obvious prototypic features for known objects in the left-hemisphere and, finally, to the discernment of object components that may by degraded, obscured, or require more detailed discrimination at subordinate level (processed in the right-hemisphere). This leads us to suppose palaeoartists were generally using the left hemisphere for the realisation of the prototypic view that incorporates the main global features (the most direct route for conscious recognition and naming). However, the right hemisphere was employed when depicting very degraded views, superimpositions (as surrogate camouflage?) or aspects of an animal dealing with subordinate characteristics.

This suggests palaeoartists, although primarily concerned with salient aspects of the familiar global form, sometimes manipulated the viewing parameters in several distinct ways in order to make visual conditions more challenging, e.g. rotation, superimposition, occlusion. The alternative lighting options of caves and shelters will have been additionally manipulated by lamp burners or fires to further enhance or degrade clarity of viewing, thereby altering perceptual thresholds for recognition allowing different but complementary recognition pathways to be stimulated accordingly. Bahn and Vertut (1997: 108) endorse this possibility by stating that such lighting alterations will have worked to the advantage of palaeoartists by causing engravings to appear and disappear to various degrees. These diverse viewing formats would have served to differentially simulate (and stimulate) the perceptual-recognition pathways as they functioned on hunting forays, thereby improving overall awareness for such forms.

Waller's comment in relation to the weakness of citing Bonnet's syndrome is relevant here. I was merely making the point that subdued lighting may have been *one* contributory factor that helped bring fauna readily to mind—the emotive aspects of interaction with animals constitutes the more essential ingredient that will have led to a spontaneous visual outpouring of animal forms. In fact, Mundkur (1988) provides examples of numerous alternative situations where animals spontaneously occur in human subjective experience in both children and adults cross-culturally, e.g. dreams, nightmares, hallucinations, imagination etc. It is the fact fauna, as a subject, of the same basic graphic format is to be found in a wide variety of settings, including shelters, open sites and on manuports that is the more substantive point that sustains my thesis. Although depictions were sometimes placed in remote recesses, many were also placed in chambers so the images could clearly be seen. This is verified by the fact that stalagmites and stalactites were often broken and removed in order to optimise viewing conditions (Bahn and Vertut 1997). Depictions placed in more inaccessible areas may have presented one extreme in a continuum of viewing alternatives, from the most challenging in this case to the optimum typical of outdoor sites.

Such observations tend to argue against Waller's favoured explanation regarding acoustics—as depictions are, first and foremost, visually mediated. Furthermore, as far as palaeoart is concerned, the fact many of the same kinds of depictions were placed in areas devoid of the resonance found in caves, such as open sites (e.g. rock faces and, occasionally, on the ground) discounts acoustics as a predisposing factor.

Eyes and deception in nature and art

Deręgowski's notion that eyes are generally absent because of the ambiguities of drawing such coplanar features does not seem sustainable. There are copious examples where eyes of animals are clearly present—though the single eye, when depicted, is often drawn in its frontal aspect rather than as in the correct profile view. Notwithstanding this, eyes are frequently omitted in the many abbreviated portrayals, possibly because the overall profile is more important for recognition in a wide range of situations.

However, Deręgowski's second point, relating to the perception of eyespots by infants and animals, is a convergent piece of research that independently supports my main thesis relating to sign-stimuli. As Deręgowski implies, deception and artifice are the rule rather than exception in nature. This can reach sophisticated levels even in the insect world; for example there is a moth, know as the Buff Tip (*Phalera bucephela*), where markings on the flat 2-D wings convincingly resemble a 3-D twig, or similarly orchids that realistically mimic a whole range of female insects. In these cases, the mimicry of one species sets out to deceive the perception of another. The fact that these perceptual tricks can work for us (though not with the same behavioural outcome) just as much as for the intended species, says a lot about how human perception meshes with the same underlying evolutionary determinants. Fascinatingly, and for the reasons outlined, this device seems to have been appropriated by early humans in palaeoart in the pursuit of self-deception!

Primitivism, and early art in relation to modern humans

This does not mean, as Heyd suggests, that I assume *Homo sapiens* responsible for palaeoart to be cognitively more primitive or inferior to modern populations because this art relied on the perceptual correlates to do with sign-stimuli. On the contrary, it is only by identifying specific traits in modern humans, which are thought to be a consequence of our evolutionary past, that we are able to draw parallels with early ancestors. Such traits include anxieties and fears to do with animals, insects, strangers, closed and open spaces etc. What ultimately appears to make modern humans different seems to be the amassing, conservation and effective modes of passing down information to succeeding generations rather than superior cognitive capacities. Culture can therefore be defined as a sideways floppy disk that can be drawn upon in a myriad of ways to artificially update and expand a common, but enduring, anciently-derived cognitive capacity that is equally applicable to present day humans as it was for Cro-Magnons. The complex social/cultural patterns, which Heyd refers to, is precisely the accumulated knowledge a community has cherished and preserved for the benefit of succeeding generations; this obviates the need to invest further time and energy in acquiring the same knowledge. Palaeolithic art will have contributed to a similar accumulative process in that important cues for the rapid identification of animal forms were preserved for the benefit of succeeding generations.

The universality of animals and typical contours

The universality of animal depictions and typical contours is questioned both by Bradshaw and Waller. Bradshaw cites the Gwion (formerly Bradshaw) paintings of Australia in this regard in that they employ silhouettes rather than outlines and primarily seem to be of human-like figures. Notwithstanding the fact that there is a continuing dispute as to whether these paintings are 17 500 BP or, as has been proposed recently, not more than 3900 BP (Watchman et al. 1997), the fact silhouettes are used does not detract from the importance of outlines. Critically, Halverson (1992b: 391) and others have shown how silhouettes are really a way of accentuating external contours that serve to highlight the difference between figure and ground. Furthermore, IRART has established that the outlines of the Gwions were drawn before application of the infill. Although animal figures are largely absent from the 'Bradshaw' (Gwion) corpus it is significant that humans constitute the major theme—as this is the second most common category found in European palaeoart. Additionally, as there are thought to be some 100 000 sites relating to these paintings, of which only a few have been documented, it remains a distinct possibility that a significant number of animal depictions will be forthcoming.

In the art of Australian Aborigines animals have always been a dominant theme. Although, as Waller indicates, Aborigines do not depict the same animals as are depicted in other parts of the world, yet they are still primarily of animals, albeit of different species. One of the common aspects of an animal's shape, as Deręgowski et al. (1996) point out, concerns bilateral symmetry that defines the spine, which normally forms the longest contour spanning the back and neck and involves curved contours. As animals in Australia would equally have evinced such curved contours it is sensitivity to the type of curves themselves that would have been the important factor. In this respect, it has been established humans are particularly attuned to the inflection of curves to the extent that they can be sensed pre-attentively (Gibson 1933; Hoffman and Singh 1997; Treisman and Gormican 1988). Thorpe et al. (1999) have even found that humans are reliably capable of sensing the presence of an animal in a picture when this is presented to extreme peripheral vision and therefore not accessible to conscious awareness. Spinal contours are eminently suitable for identification of animals from a range of distances, angles and situations and therefore are a robust qualitative feature engendering ease of recognition. So it is not so much tusks, antlers, horns, spinal contours etc. themselves that are the defining parameters, but the fact these are curved and to which the human perceptual system has evolved to be especially attuned. This is validated by the fact animals in typical outline view are an overwhelming feature of world rock art horizontally and vertically through time, e.g. Kennedy and Silver (1974). Moreover, palaeoartists often overpainted or further engraved the outline, especially the dorsal contour, thereby accentuating its importance. As for Australian fauna, Smith (1998) has shown how the same perceptual criteria to which Deręgowski and I allude can be equally applied to this sample.

Waller suggests that there is no way to prove visual defined templates were being used to produce palaeoart, but this ignores the fact the authors concerned would have been incapable, in the first instance, of producing such representations without these very same determinants. There is a hierarchical framework for such visual realised outlines. For natural categories the most general begins with the superordinate (e.g. animal), followed by the basic—most natural and easily accessed level (e.g. antelope), to subordinate—for exemplars (e.g. gazelle, impala, eland), respectively. According to the level that needs to be accessed for the purpose of identification, each has its own signature relative to the amount of visual information required, which is mediated foremost by the typical outline contour (Tversky and Hemenway 1984). Brain damage can lead to the selective sparing and loss of any one of these categories, with the superordinate being the most resilient whereas the subordinate constitutes the more vulnerable (Logothetis and Sheinberg 1996).

Kehoe's commentary cites converging evidence from cognitive linguistics that supports the concept of sign-stimuli and usefully supplies documentation regarding the universal nature of animals in various cultures. I commend Kehoe for the interesting observations regarding Lakoff as well as those of Ingold and others—to which I refer Bradshaw and Waller in relation to the question of universality.

Top-down perceptual processes and hypothesis testing

Both Waller and Deręgowski emphasise the importance of Gregory's notion of hypothesis testing. Although Gregory admits certain evolutionary factors are important in perception his approach is predicated on the empiricist notion that most of our perceptual faculties have to be learnt from scratch (Gregory 1974b: 613). However, Gordon (1989) raises questions relating to the consistency of Gregory's position by pointing out that the world is common to all perceivers, therefore where does this come from if each individual has to construct a personalised, idiosyncratic world? From this perspective, Gregory's hypothesis testing can be re-interpreted as a predisposition to question uncertainty and, as uncertainty represents a threat, this needs to be identified as rapidly as possible. Other aspects of Gregory's general approach have been likewise questioned. To reiterate, perception evolved by dint of a long experience of past environments that predated modern human civilisation—it is this past experience, as embodied in the visual brain, to which we are still obligated. Bradshaw reinforces the concept in stating that there are no specific perceptual adaptations which greatly distinguish us from our hominid ancestors. This is further substantiated by the fact that, compared to other mammals and primates, no new evolution-derived structures are to be found in the human brain (Holloway 1999).

Derek Hodgson
2 Belle Vue Street
York
North Yorks YO10 5AY
England, U.K.
E-mail: *dhgson@email.com*

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