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THE BODY AND THE BRAIN: NEUROSCIENCE AND THE REPRESENTATION OF ANTHROPOMORPHS IN PALAEOART

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Abstract. Previous studies on palaeoart employing a neuroscientific perspective have focused largely on the representation of animals. Anthropomorphs are one of the most common subjects depicted in palaeoart worldwide, yet the understanding of this category of imagery has not benefited from such an approach. This paper demonstrates how an understanding of inherent aspects of human neurophysiology and visual perception may help to explain the derivation and persistence of anthropomorphs in rock art and portable art around the world, and contribute to explaining ways in which they are commonly portrayed. It considers the significance of recent neuroscientific data in understanding how the human body is processed and represented in the brain and the influences this has on its graphic representation.

Introduction

Anthropomorphs are particularly common in palaeoart worldwide.¹ Overall, they are probably the second most common figurative subject depicted after animals. Some rock art traditions, such as the Gwion Gwion (Bradshaw) paintings of the Kimberley region of north-western Australia (e.g. Walsh 1994, 2000), or the drawings and paintings at various sites throughout eastern Australia (e.g. those in central western and south-eastern New South Wales: McCarthy 1976, Officer 1991), are almost entirely of human subjects, represented in a wide range of forms. Human figures comprise more than half of the figurative paintings in other regions of the world, such as Namibia (Le Quellec 2004: 155) and the Drakensberg area of South Africa (Vinnicombe 1976), among many others.

Despite the great diversity of human or human-like figures (e.g. Clottes 2002, Ucko and Rosenfeld 1972), including isolated body parts such as heads, hands

and sexual organs, there are several characteristics of anthropomorphs that are found across temporal and geographic domains. Some of these characteristics include the schematisation of human form as stick figures and silhouette figures (Figs 1 and 2); their sketchy or unrealistic representation; the exaggeration of certain features; and the sexual nature of some imagery (Fig. 3). A number of scholars have suggested that the nature of this imagery has been influenced by human perception and the properties and tendencies of the visual system (e.g. Barry and White 2004; Bradshaw 2006; Deręowski 1996, 2004; Hodgson 2003; Hodgson and Helvenston 2006; Watson 2009, 2011). Despite this, anthropomorphs as a category of imagery has not benefited from a neuroscientific approach to the same extent as those studies focusing on the representation of animals (e.g. Hodgson and Helvenston 2006).

This paper argues that an understanding of inherent aspects of human neurophysiology and visual perception may help to explain the derivation and persistence of anthropomorphs and contribute to explaining ways in which they are commonly depicted. It focuses on some of the most common types and characteristics of anthropomorphous imagery worldwide. In doing so, similarities in the portrayal of basic human form are shown to be independent developments rather than the result of cultural diffusion, especially when human representations are highly schematised (Brandl 1977: 225; Ucko and Rosenfeld 1972: 174) (but not, perhaps, in cases involving similar highly stylised or detailed forms

¹ The term 'anthropomorph' is used here to refer to 'an object or picture providing adequate visual information to most contemporary humans as resembling human form' (Bednarik et al. 2010: 2). It thus includes pictures of objects that look like humans but may have been intended by the artist to represent something different, perhaps mythical or supernatural in nature. The definition employed is intended to reflect the fact that pictures on their own are not known to be pictures of things, i.e. depictions or representations, unless ethnographic data is available for their interpretation. The distinction between what can be directly observed and what is interpreted is important to some rock art researchers (e.g. Clegg 1988), but not others.



Figure 1. Painted stick figure anthropomorphs from Cadell River, northern Australia. Note group of very simple stick figures at right (after Brandl 1977: 228).

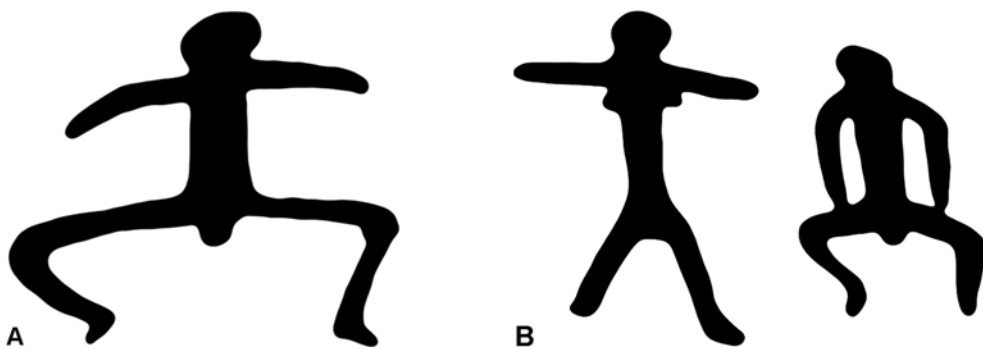


Figure 2. Painted silhouette anthropomorphs from Mulgowan (A) and Mt Grenfell (B), north-western New South Wales, Australia (tracings of photographs by David Watson and the author).

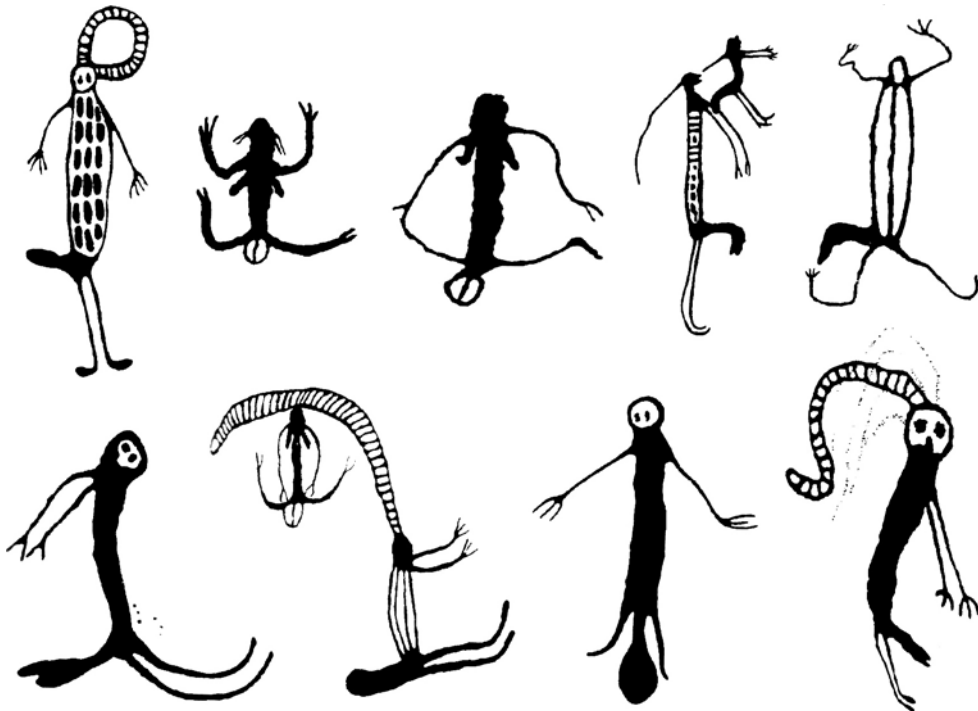


Figure 3. Examples of anthropomorphs with exaggerated sexual features: Woodstock figures (petroglyphs) at Gallery Hill, Pilbara, north-west Western Australia (after Mountford 1965: 99).

and where cultural contacts can be clearly demonstrated). More convincing explanations are also provided than other simplistic theories, such as the ubiquitousness of stick figures being a result of economy of time or effort (e.g. Wright 1977: 111), or difficulties in the depiction of human form, which do not account for many highly detailed and skilfully produced paintings and engravings.

Recent neuroscientific studies are considered in terms of their significance for understanding how the human body is represented in the brain and the subsequent influence this has on its graphic representation. Specialised neural structures for the visual processing of human bodies and their parts have developed because of the great importance of those aspects of humans in social life and communication. The human body and its parts are considered high-level 'aesthetic primitives' (Latto 1995: 86) or particularly 'powerful' visual images

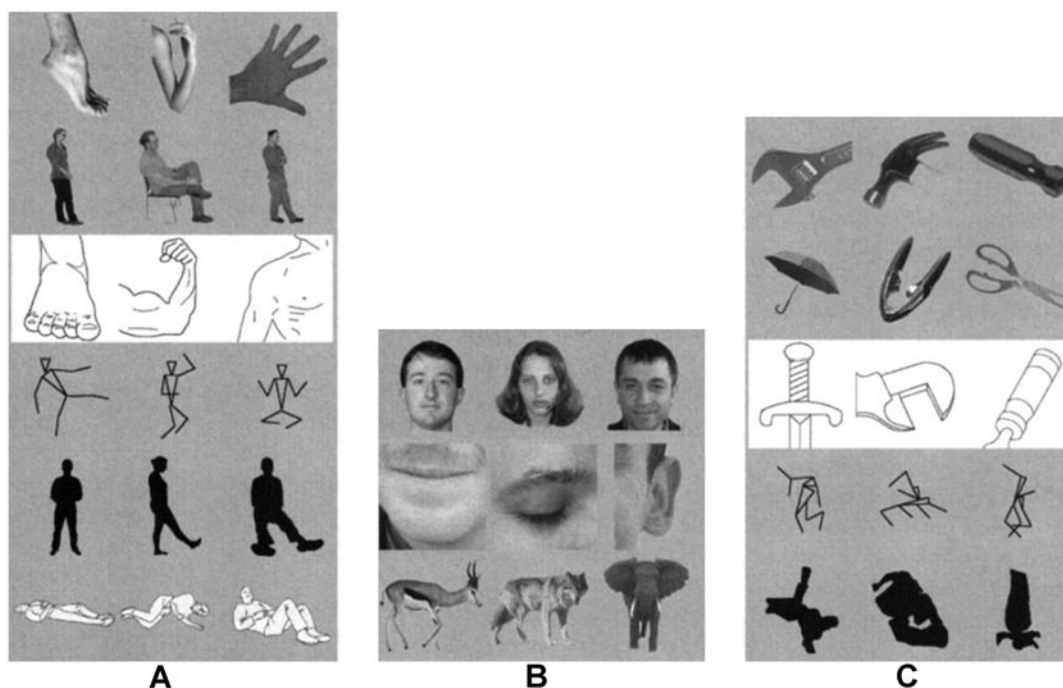


Figure 4. Examples of stimuli used by Downing et al. (2001). EBA response was high to stimuli in column A, intermediate to those in column B, and significantly lower to those in column C (from Downing et al. 2001: 2471, adapted and reprinted with permission from Paul Downing and AAAS).

that are capable of evoking a form of 'aesthetic' response by activating neural pathways that are specifically attuned to processing these forms. This response can be interpreted in terms of visual attention and neurophysiological response or arousal. These factors may help to explain why palaeoartists throughout the world were preoccupied with depicting the human body and its parts, and portraying them in certain ways.

Visual processing of the human body

A constant and inescapable visual experience, the human body is a particularly special object of perception (Knoblich et al. 2006). Interest in the neural basis of human body perception has increased enormously with the development and use of brain imaging (Peelen and Downing 2007). Brain imaging studies have recently revealed the existence of predetermined structures for body perception and representation. These structures are located in approximately the same anatomical position in all normal subjects and are part of the basic functional architecture of the brain. The perceptual and cognitive processes underlying human body perception both inform and can be informed by graphic representation of the body (Reed et al. 2006). Accordingly, the relationships between the human body and perception provide important insights into the depiction of anthropomorphs in palaeoart.

Functional magnetic resonance imaging (fMRI) studies reveal evidence for a distinct cortical region in humans that responds strongly and selectively to static images of human bodies and body parts (Downing et al. 2001; Peelen and Downing 2007). This is located in

the posterior inferior temporal sulcus, and has been named the extrastriate body area (EBA). The EBA is separate and distinct from neural systems involved in the perception of faces and nonhuman objects such as tools, allowing for specialised categorical processing of the human body. Importantly, it responds strongly to pictures and photographs of parts of the human body, including the eyes, ears, feet, hands and elbows, as well as the body as a whole, including silhouettes, artist's renderings and stick figures (Fig. 4). It responds less to similarly shaped inanimate objects and stick figures arranged in such a way that they no longer resemble a human shape. This observation suggests that the EBA represents the body in abstract form (Downing et al. 2001; Peelen and Downing 2007: 638), which may partly explain the tendency for palaeoartists to produce generalised depictions such as stick figures and silhouette figures (see below). Most, if not all stimuli used by Downing et al. (2001) that received a high response by the EBA may be found in rock art (although some are more common than others), which may reflect the neurological stimulation they afford.

fMRI studies have further demonstrated that an anatomically distinct brain region located in the fusiform gyrus, the fusiform body area or FBA, also responds selectively to human bodies and body parts (Peelen and Downing 2005a; Schwarzlose et al. 2005). Significantly, the FBA not only responds selectively to whole bodies and body parts, but like the EBA, also responds selectively to schematic depictions of the human body, including stick figures (Peelen and Downing 2005a). These two brain areas do not function identically, and there are significant differences between

them. By measuring the magnitude of fMRI response, Taylor et al. (2007) found that EBA selectivity increased relative to an increase in the portion of a human figure visible in a given stimulus (ranging from a single finger to the entire body). They also showed that the selectivity of the EBA increased when more of the body was shown, whereas the FBA did not show selectivity for individual fingers or hands. It is thus thought that the EBA is concerned with analysing bodies in relation to their parts, whereas the FBA is concerned with organising parts of bodies into wholes.

These findings could well be relevant to questions of the recognition of anthropomorphous form or potential anthropomorphous form by early hominins in naturally occurring objects, as well as their further intentional enhancement. This is apparent in the object from Berekhat Ram, Israel — an engraved scoria pebble from a Late Acheulian occupation level minimally dated to c. 233 000 years ago, and possibly as old as 800 000 years (Goren-Inbar 1986; Marshack 1997a). Experimental data from d'Errico and Nowell's (2000) studies, as well as Marshack's (1997a, 1997b: 60) microscopic analysis, suggest that it was intentionally modified by early humans in a number of ways, including shaping and bevelling, scraping, smoothing and grooving, to enhance and emphasise the natural human-like form. Contemporary with the Berekhat Ram figurine is the similar object from Tan-Tan, southern Morocco (Bednarik 2001, 2003). Again, the figurine is a naturally shaped but humanly modified and enhanced object, in this instance of quartzite. This was recovered from a Middle Acheulian occupation deposit dating to between c. 300 000 and 500 000 years ago. This object also features intentionally engraved grooves, produced by pressure or careful percussive force. The shape of the object suggests iconic recognition on part of the hominin responsible, as the grooves emphasise the natural iconic form and symmetry of the object (Bednarik 2001: 115, 2003: 409).

Evolutionary considerations

Humans are highly social animals, and the perception of self and others is of obvious importance to the survival of the species. In this sense the perception of others and the existence of specialised neural mechanisms for processing the human body and its parts is a necessary condition of visual awareness and mental representation. fMRI studies have suggested that regions of the brain selectively responsive to stimuli of a particular class that are not likely to be subject to evolutionary pressures (such as words) may develop as a result of experience, rather than evolutionary processes and genetic predispositions (Baker et al. 2007; Cohen and Dehaene 2004; Polk et al. 2002; Puce et al. 1996). It can reasonably be assumed, however, that hunter-gatherers in the past were highly dependent on conspecifics and that these brain regions developed universally. The cortical regions discussed undoubtedly existed in the brains of palaeoartists who produced

anthropomorphous imagery. As Downing et al. (2006: 1459) have pointed out, specialised cortical areas for bodies and faces may exist because of the importance of conspecifics in survival throughout the evolution of the species and because of the extensive exposure individuals have to other people throughout their lives. The cortical organisation involved appears to be restricted in its modification and largely genetically determined (Krubitzer and Kaas 2005), although additional research is needed to understand its evolutionary origins (Peelen and Downing 2007: 646).

Familiarity with hominin form throughout evolution and the response to highly social information in its ability to capture attention attest to its visual salience (e.g. Langton and Bruce 2000). For example, Downing et al. (2004) tested body and non-body stimuli (silhouettes and stick figures of human bodies) showing that simple images of the human body are more likely to be visually detected and significantly better detected by observers than other stimuli, suggesting that the human body is prioritised for attention, including representations of bodies and body parts (see also New et al. 2007). This further suggests that the human form is more important or meaningful than other visual stimuli. The brain imposes selectivity on the human form, acting as a bias in its depiction and the importance given to such forms, based on the existence of underlying categories of perception.

Human bodies convey much information that is highly relevant to social life and survival. Not only recognition, but observation, imitation and interpretation are essential to the representation of self to others in primate social interaction and communicative behaviour (Burton 1992: 42–44). For the human species and higher primates generally, perhaps the greatest threat is from conspecifics, as opposed to predatory animals (Bradshaw 2006). It follows that one of the most important functions of vision in humans is the provision of information about conspecifics, including their identity, actions and mental states. In a hostile environment, social cohesiveness would have been essential to the survival of early humans. For example, group cohesion would have made individuals less vulnerable to attack from outsiders and predatory animals, and improved chances of finding food. The need for positive social interaction in human evolution is thus imperative to understanding the importance of the human form and human features in the brain, and subsequently the management of social information resulting in artefactual activity (Chase 2001). Humphrey (1984, 1986) considers social interaction, rather than tool use, as of primary importance in hominin cognitive evolution. The social behaviour characteristic of primate life requires the highest intellectual faculties for appropriate social skills, such as the calculation of behavioural consequences (Humphrey 1984). Social life also requires complex problem-solving abilities, memory, and mental templates for such abilities as distinguishing individuals (Calvin 1996: 67). The

capacity for the latter is clearly evident in human infants, suggesting inborn factors at play (Johnson and Morton 1991). Other abilities, such as rapid analysis of body posture and movement in social situations are also vital in an evolutionary context, as are the recognition of faces, facial expressions and the direction of gaze (Barrowclough 2004: 104).

Understanding humans as both predator and prey emphasises human co-operative instincts and co-dependence (Hart and Sussman 2005). This is important to understand from an evolutionary perspective, as the close genetic and evolutionary relationship between chimpanzees and humans (Chimpanzee Sequencing and Analysis Consortium 2005) has important implications for understanding human behaviour. Studies on wild chimpanzee hunting behaviour and ecology provide significant insight in relation to early hominins and the development of a visual system highly attuned to anthropomorphic forms. Chimpanzees regularly hunt to obtain meat. At Gombe National Park, Tanzania, for instance, colobus have been reported to comprise more than 80 per cent of prey (Stanford 1995). Fossil deposits indicate that the Pliocene forested environment chimpanzees inhabited was also shared by colobus monkeys (Stanford 1995), and it is highly likely that early hominins hunted monkeys in much the same way as modern chimpanzees. Substantial evidence exists for killing and cannibalism among modern primates (Bygott 1972; Goodall 1977), as well as early hominins and the genus *Homo* in the archaeological record (Cole 2006). It is probable that early humans were hunted by other primates with which they coexisted, and vice-versa. The persistence of human conflict throughout history may also be significant in relation to environmental stimuli activating innate response mechanisms and the appearance of anthropomorphic imagery in palaeoart.

Stick figures and the schematisation of human form

Human vision is an active process of extraction and simplification of those features of the world that are most relevant to survival and most necessary for the categorisation of objects. Abstraction is a process where particular features are generalised, enabling the rapid and efficient acquisition of information by the brain (Zeki 2001: 52). This is a fundamental capacity of the visual system, with a basis in the flexibility of processes in the anterior part of the inferotemporal cortex responsible for aspects of object recognition (Tanaka 1996). Abstraction by the brain is reflected in the characteristics of representation in art whereby aspects of the ever-changing visual world are simplified. Humans often simplify or idealise things in depictions, and the portrayal of objects with very few structural features is particularly prominent in palaeoart (see Ucko 1977). For the purpose of two-dimensional representation, the schematisation of objects is achieved by the use of line (in one form or another), and this is universally

employed in drawing (Kennedy and Silver 1974; Latto 1995). As noted, the independent development of this form of depiction can be partly explained as a result of the selective response of regions of the brain to certain forms of imagery, including schematic representations of human form (Latto 1995: 89).

Evidence for the ability to abstract important features and to reproduce them in palaeoart reflects the longevity of the cognitive and motor skills required (Deręowski 1984: 25). The engraving on a bone fragment from Oldisleben, Germany, attributed to a Micoquian context and dating to c. 80 000 years ago (Bednarik 2006), may be amongst the earliest figurative depictions in the world. The markings on this object strongly suggest the schematisation of human form into the most basic of representations. Generally, however, figuration (including schematised anthropomorphic imagery) is found much later, beginning in the Upper Palaeolithic.

The schematised representation of animal and human forms into 'stick' or 'pin' figures is a ubiquitous graphic device found in palaeoart petroglyphs and paintings throughout the world. These are designs that depict humans and other animals in their simplest form, depicted with thin lines. According to Brandl (1977: 226), the prototypical human stick figure cannot be further reduced or simplified without becoming unidentifiable as a human form: 'four lines seem to be the irreducible minimum: a horizontal one for the outstretched arms, a vertical one for head and body and two lines for the legs, starting at the lower end of the trunk, usually (but not necessarily) at an angle to one another'. The relatively simple arrangement of limbs in humans allows their representation as simple stick figures and undoubtedly contributes to the tendency towards this form (Deręowski 1984: 47).

Examples of stick figures approximating Brandl's prototype include those from a site on the Cadell River, Arnhem Land, northern Australia, having been painted in thin single lines (cf. Fig. 1.). These stick figures still have more traits than the prototype he has defined (in that circles are used for the heads and two lines are used for the arms rather than one). There are countless examples (both pictograms and petroglyphs) around the world (see e.g. Fein 1993: 76, 122). Brandl's prototype, however, is not as common as those stick figures with some form of attributed feature, be it the widening of body and limbs, the addition of material culture (commonly weapons), or other alterations. Even in the simplest representation of humans some variation of design is likely, and different styles or elaborations of the simple stick figure are widespread (e.g. Rusco 1973). Stick figures are not free from cultural influence, although the same basic means of graphic representation are used, resulting in close resemblances between those of different cultures (Deręowski 1984: 25).

Stick figures comprise one form of epitomic depiction (where depiction is devoid of perceptible depth)

(Deręowski 1995). In terms of visual perception they are essentially an abstraction, the simplistic structure of which is easy to recognise and recall. To some extent, abstraction may simply result from the fact that there is no need to recall every detail of objects, particularly those as familiar and perceptually salient as the human form (Zeki 2001: 52). Stick figures are easily produced, and easily perceived by all normal humans. Even among pictureless or relatively pictureless societies such as the Songe of Papua New Guinea, highly schematic human figures have been shown to be easily identified, emphasising their 'pictorial efficiency' and the fact that the use of line is easily understood by the human visual system (Kennedy and Ross 1975: 402; Kennedy and Silver 1974: 320). Human representations drawn by people from pictureless cultures who have never drawn before, such as those by the Tallensi of northern Ghana, produce extreme versions of stick figures (although gender is clearly recognisable) (Deręowski 1978, 1984: 47-48, 1989; Fortes 1940, 1981; see also Martlew and Connolly 1996).

The drawings of children are also important to consider, as the prototypes that follow from the scribble phase of drawing during a child's development do not appear to be influenced by culture. Rather, they represent a reduction of essential features following the generalisation of essentials, which is more basic than the inclusion of detail (Sütterlin 2003: 148). In accordance with Gombrich's (1977) thoughts on 'primitive' art, children also tend to 'draw from knowledge' or the conceptualisation of an object as opposed to drawing from the direct observation of an object (Arnheim 1966: 29; Davis 1985; Freeman and Janikoun 1972), strongly suggesting the existence of inherent processes acting as a bias in governing the production of stick figures in drawings.

Stick figures in palaeoart are largely impersonal, lacking particularity, and generalised in schematic form; they are reduced to a 'universal human' representation that may or may not be differentiated by indication of sex. (This is not to say that a stick figure was not created for the purpose of representing a specific individual, which is clearly the case in children's drawings and some instances of rock art [Smith 1995; Taçon 1995].) In some cases, social and sexual 'identity' (Fisher and DiPaolo Loren 2003) or 'socio-sexual signalism' (Wickler 1967) may be represented by the addition of details that distinguish between the sex of a figure or other features. The development of standards in the ways in which figures and their fundamental features are portrayed is a typical response by cultural groups to problems faced by graphic representation (Chippindale 2001: 259), particularly those arising from the perceptual instability of the human form resulting from the highly variable nature of its typical contours (see below). The use of a standard set of conventions results in one aspect of a culturally specific style. Perhaps the best example of this is the standardisation in the style of human representation in ancient Egyptian art (Gombrich 1950;

Shäfer [1919] 1974). In contrast, many of the similarities observed in rock art and portable art lack a degree of standardisation between groups, giving rise to common forms.

Principal axes

The recurrence of basic schematised anthropomorphs based on main axes of body and limbs is well explained as psychological in origin. Arnheim (1974: 93) has noted that there are two main properties of visual objects in relation to 'shape'. The first includes the actual boundaries produced by the artist (lines, masses, and volumes), and the second the 'structural skeleton' (Arnheim 1974: 92-95). When the human form is reduced to its basic shape (as in stick figures), the concept of a human is immediately recognised. It is most likely that depiction of principal axes is so effective because it corresponds to the simplifications made by the visual system in analysis and representation and is processed more efficiently. According to Arnheim (1974: 93, 123) (in accordance with Gombrich's notion of 'conceptual representation' and the ways children draw objects discussed previously), 'the guiding image in the artist's mind', which is essentially the structural skeleton of an object, to a large extent determines (or is at least reflected in) the nature of the depiction. In other words, the artist is constrained by the internal representation of the human form governed by underlying information-processing mechanisms. Interestingly, this observation was made before the development of neuroimaging techniques and subsequent studies suggesting that humans are represented or encoded in the brain in schematised form.

In relation to the structural skeleton of objects and the representation of humans as stick figures, the principal axes or axes of symmetry of objects is a particularly important concept. Stick figures are depicted by their principal axes around which parts of the whole are grouped in the construction of form. Supported by data from neuroscience, they are a form of imagery capable of evoking particularly strong perceptual responses. As noted, objects including humans and animals depicted by their principal axes serve as sufficient representations, and despite having no surface information they are easily recognisable. Representation based on principal axes of objects is demonstrated well in the construction of pipe cleaner models of animals, where the pipe cleaners stand for the axes of volumes (Marr 1982; Marr and Nishihara 1978) (Fig. 5). These models are easily recognisable despite the absence of information about the surface of their shape. This suggests that a broad class of structures can be represented by highly schematic forms characterised by essential features, reflecting the constraints by the brain in the categorisation of structures in patterns. The processes involved in recognising these object-centred representations are not fully understood, but Marr (1982; Marr and Nishihara 1978) has suggested that they involve the categorisation of component



Figure 5. Marr's pipe cleaner models of animals (from Marr and Nishihara 1978: 271 [Figure 1], reprinted with permission of the Royal Society).

parts. Similarly, Hoffman and Richards (1984) suggest that three-dimensional objects are segmented into component parts by perceiving contours. This is in accordance with the notion that the skeletal structure of an object is generated at an early stage of visual processing (Kovács 1996).

Silhouette figures

In addition to stick figures, anthropomorphs are also commonly depicted in silhouette or outline form (cf. Fig. 2). Principal axes also serve as a structural basis for the generation of silhouette figures. In this sense, silhouette figures may be understood as stick figures that have been 'fleshed out' to create visually realistic contours. Despite the difference in the level of abstraction between stick figures and silhouette figures (Parker and Deręowski 1990: 227), silhouette figures do not require shading or other embellishments to be identifiable as anthropomorphs. Parker and Deręowski (1990: 227) have argued that stick figures may be more easily recognised than silhouette figures of this type. However, the fMRI study conducted by Downing and colleagues (2001; see also Peelen and Downing 2007) found that the EBA response was also very high for body silhouettes and whole bodies. This

may not be particularly surprising considering that silhouettes are closer to the veridical human body in their representation. The fact that enhanced stick figures or silhouette figures are particularly common in palaeoart accords with this finding. In addition to being schematised in the sense that they often lack any infill detail or facial features, silhouette figures are based on the same principal axes and act on the same neuro-perceptual mechanisms as stick figures.

In addition to ease of recognition, human preferences for symmetry, including the attractiveness of symmetrical faces and bodies (e.g. Grammer and Thornhill 1994), might partially explain why stick figures and silhouette figures (and anthropomorphs generally) are commonly depicted in frontal view. Some rock art corpora have a much greater percentage of anthropomorphs depicted in lateral view. For example, in the art of Ndedma Gorge, southern Africa, 98 per cent of anthropomorphs are depicted in lateral view, and only two per cent in frontal view (Pager 1972). For others, such as the silhouette figures of the Cobar Pediplain in western New South Wales, Australia (McCarthy 1976), quite the opposite is the case. As in the examples of representations of humans by individuals from cultures with no experience with representational drawing, anthropomorphous depictions include all necessary information required for the recognition of a human (or human-like) figure. Importantly, these are composed on the basis of a vertical axis, clearly discriminating extremities. It is typical that only the most basic variation on the symmetrical prototype based on the vertical axis occurs in palaeoart, with all other characteristics omitted, so that abstraction takes precedence over realism. This may best be explained in terms of perceptual processing and prototypical templates (Sütterlin 2003: 151). The prevalence of human representations based on this prototype supports the notion that the origins of this concept are found in shared human perceptual-neurophysiological mechanisms. Good examples of the use of bilateral symmetry according to this fundamental perceptual template include depictions of humans in various parts of the world (see e.g. Bahn and Vertut 1988; Patterson 2007: 350; Vinnicombe 1976). Examples of bilateral symmetry are also seen in the often prominent depiction of eyes in anthropomorphous faces (Watson 2011). The perceptual determinants responsible may ultimately account for the appearance of these figures and explain the apparent preference for these forms of human representation.

Incomplete figures

Another common feature of anthropomorphs in palaeoart is their apparent 'incompleteness'. Examples include those in Upper Palaeolithic Europe (Ucko and Rosenfeld 1967, 1972), such as many of the anthropomorphs depicted in profile at Gönnersdorf, Germany (Rosenfeld 1977: 98); and those in Arnhem Land, northern Australia (Gunn and Whear 2007). In

Palaeolithic Europe, the parts of the body most often depicted include the head, trunk (the middle parts of the body including the chest, pelvis, and thighs), sexual organs, and hands (Lorblanchet 1989: 130–133). Incomplete anthropomorphs may be reduced to only the trunk, a form that emphasises the disregard for the head and face (Lorblanchet 1989: 133). More than half of all anthropomorphs with torsos in Palaeolithic Europe occur without any arms (or obvious arms) (Ucko and Rosenfeld 1972: 182), and a high proportion also lack detailed facial features. This has been suggested to be a result of the use of pigment or clay that has not withstood taphonomic processes (Graziosi 1960: 88; Ucko and Rosenfeld 1972). Gunn and Whear (2007) have suggested further reasons that may have prevented the completion of paintings and petroglyphs in Australia. These include the time required to complete a figure; the need for a sufficient amount of pigment; or interruptions by other people, hunting opportunities, or changing weather conditions (Gunn and Whear 2007: 26).

Alternatively, incomplete figures or the depiction of their parts may be understood as reflecting the functioning of innate human perceptual-neurophysiology. Although there are similarities between brain regions, there are clear functional and anatomical distinctions between the neural systems involved in processing the body and isolated body parts, and the face (Downing et al. 2001; McCarthy et al. 1999; Pourtois et al. 2007). The extrastriate and fusiform body areas, for example, are known to respond selectively to images of the human body without the face (Peelen and Downing 2005b; Schwarzlose et al. 2005). This may partly explain the often faceless and headless anthropomorphs in palaeoart, in that the artists exploited one type of visual stimuli that provides a strong affective response.

Many anthropomorphs are only identifiable by distinctive, diagnostic anatomical features (e.g. pubic triangle, penis, arms, hands or feet) added to a highly schematised or incomplete form (Ucko and Rosenfeld 1967: 156). Although sufficient visual information is required for configural processing so that the general structural organisation of the human body can be reconstructed by the brain, a complete template or identical match is not required (Reed et al. 2006: 239, 245). This relates directly to the Gestalt perceptual principle of closure, where a partly obscured form or figure tends to be perceived as though it were complete (see Shimaya 1997 for a review of figural completion theory).

Significantly, cross-cultural studies have shown that the Gestalt principle of closure is based in innate perceptual-neurophysiology and not dependent on cultural factors (Michael 1953). Human figures that are partially incomplete or obscured may therefore still look like a whole person (Pickford 1976: 157). They may be well identified in partly occluded or 'noisy' scenes (such as rock surfaces) because their symmetry is more predictable than asymmetric forms (Rappaport

1957; Wolf and Friedman-Hill 1992). The principle is readily applied to palaeoart and may have been unconsciously employed by those who produced it. Like Michelangelo's unfinished sculptures, 'incomplete' human figures in palaeoart may be interpreted as intentionally unfinished (Zeki 1999: 31, 2002: 65–66). In this sense, palaeoartists may have exploited (consciously or intuitively) a type of 'neurological trick' whereby the brain is forced to imagine the finished depiction where form is elusive. This involves matching stored representations of constant features of objects with memories of what has been previously seen (see Bailey 2007: 116). It also relates to pattern recognition and the perceptual tendency to complete a pattern by visualising what is not present, as in some visual illusions such as Kanizsa's triangle. Neurons in area V2 of the visual cortex are demonstrated to respond to illusory contours in Kanizsa-like figures as they do to real contours in the reconstruction of a whole from parts (Baumgartner et al. 1984). The completion of incomplete figures in the mind's eye is also thought to be a function of the right hemisphere (Zaidel 2005: 140), and in terms of human figures, undoubtedly involves selectively responsive body areas of the brain (including the EBA and FBA) (Downing et al. 2001; Peelen and Downing 2007; Taylor et al. 2007).

Unrealistic representation and exaggeration

The range of anthropomorphs in palaeoart of the world is quite broad, yet they commonly do not reproduce the human form in a faithful way. In fact, images of humans in art throughout time and space are typically unrealistic (Spivy 2005). Although some are very finely executed, such as the detailed, accurate bas-relief figures of Laussel and the 'reclining' figures at La Magdalaine, France, many human representations give the impression of rough sketches. Those of Palaeolithic Europe, for example, are often 'crudely' or 'clumsily' represented in comparison with many animal representations (Ucko and Rosenfeld 1967: 38). As Lorblanchet (1989: 137) has noted, it is intriguing that there are so few human figures that are 'fully realistic'.

Deregowski (1996, 2004) argues that the reason why humans are often sketchily or inaccurately represented in rock art is because there are specific difficulties associated with their depiction. In other words, he argues that people are less able or incapable of depicting the human form accurately. The basis of this argument is that the human form is perceptually instable because of its highly variable nature and the changing of its typical contours. Humans change shape significantly depending on whether they are standing, squatting, sitting or doing any number of other things. This makes it difficult to find a line that represents a human, which is generally not the case with animals, particularly equines and bovines, because there is much less variance in shape and stability in their typical contours.

For Deregowski (1996), typical contour is also the

main factor determining difficulties in the depiction of some animals; because of the variability of typical contours of some animals (the cat is one example Deręowski cites), it is not possible to find a stable representation of their shape (see Deręowski 1995 and *RAR* Comments and Reply). It follows that in the small number of cases where human figures are not epitomic (i.e. have perceptible depth), as in the case of animals, they may also be depicted in lateral view, incorporating typical contours (Deręowski 1995: 7). With these points in mind, it might be argued that an inherent difficulty in the realistic depiction of human form contributes to their schematisation, with an ultimate basis in perceptual tendencies.

Hodgson (pers. comm. 2007), however, is sceptical of Deręowski's argument. There are two main reasons for this scepticism. The first is that the example of felines Deręowski argues as having a similarly complex typical outline are in fact depicted in the Upper Palaeolithic with great accuracy and realism. It is clear that Upper Palaeolithic artists were perfectly capable of portraying many animals with great skill and accuracy, and in diverse media. The capability and skill required for the depiction of human figures and faces were evidently available to the artists concerned. This observation has in fact been stressed for decades (e.g. Bégouën 1926; Lorblanchet 1989), and is clearly apparent in the engraved faces of La Marche, France. Furthermore, in modern art circles it is generally thought that it is harder to draw a good horse, for example, than a good human (R. G. Gunn pers. comm. 2008).

Deręowski (1996) further argues that the difficulties in the depiction of the human form are reflected in the relative infrequency of its depiction. This may be true for the parietal art of Upper Palaeolithic Europe, but it is not the case elsewhere, and does not explain the prevalence of anthropomorphs in the rock art of other regions. The human form is clearly found in various regions of the world, and varies in nature from static to dynamic stick figure representations (Bradshaw 2003: 10). Other explanations, particularly the role of cultural, personal or technical factors have been suggested. For example, Graziosi (1960: 183) has suggested that the human form may have intentionally been portrayed in an imperfect, impersonal manner. Vinnicombe (1976: 139-141) also suggests an unwillingness to portray the human form realistically. This might be the case in accordance with current tastes (Russell 2006: 46). Changes in archaeological sampling have also been suggested (Ucko and Rosenfeld 1972: 197). But these explanations are also largely unsatisfactory, and the typically unrealistic representation of human form can be better explained by a number of factors relating to human visual perception.

The principle of exaggeration or 'peak shift' (the neurologically inherent propensity to exaggerate) offers a compelling explanation (see also Hodgson 2003; Watson 2009 for discussions of the phenomena in relation to zoomorphs). This is evidenced particularly

in the creation of grossly exaggerated features of the human form that appears in many regions of the world throughout time (Ucko and Rosenfeld 1972: 170). The natural response in humans to certain visual stimuli is increased by the exaggeration of certain characteristics (Latto 1995: 88). When a particular stimuli is isolated and exaggerated, such as the eyes represented schematically as concentric circles (Watson 2011), perceptual mechanisms underlying the supernormal response are activated. Due to the principle of exaggeration, certain features of the human form tend to be exaggerated in its depiction. The reason for this is that exaggerations and distortions stimulate the brain's aesthetic response to the human body (i.e. the activation of neuronal responses), creating supernormal stimuli. This is a natural tendency because the brain is 'hard-wired' to give more attention to those objects (or parts of objects) that are particularly important and generate pleasing reactions.

The effect may also be achieved by the depiction of the human body in motion (Watson 2010a). Representation of axial structures and movement is a very common feature of human representations in visual arts (Jung 1987), and movement is portrayed in very similar ways across cultures, such as the use of multiple images or the positioning of limbs. Brandl (1977: 225) has noted that one of the most striking similarities in the depiction of human form in rock art is 'vigorous movement', including the widely straddled positioning of legs that is almost identical in examples of pictograms from around the world. Pictures of objects (especially pictures of human bodies) may convey the illusion of movement to the extent that predictions can be made about that motion (Reed et al. 2006: 243). The ability to perceive human motion in static depictions (including those of cultures other than our own), is dependent upon area V5 of the visual cortex that is specialised for its detection (and motion generally) (Kourtzi and Kanwisher 2000; Newsome and Pare 1988; Proverbio et al. 2009). Experiments using point-light displays (schematic representations of biological motion comprising moving sets of dots) and other forms of schematic representation demonstrate that the perception of minimal motion information is required to discern structural information about observed human bodies (Johansson 1973; Peterhans et al. 2005; Reed et al. 2006; Thornton 2006a). Recognition of this information is much greater in the observation of humans or human-like stimuli than other animals or animal-like stimuli (Shiffrar 2006: 141). In fact, a range of information can be extracted from 'form-degraded dynamic patterns' such as gender (Koslowski and Cutting 1978; Thornton 2006b). Primate studies further reveal that two main neural systems are dedicated to the perception of motion in living beings. These include neurons in the superior temporal sulcus that selectively respond to movement of bodies, body parts and faces (Allison et al. 2000; Grèzes et al. 2001; Perrett et al. 1982, 1985), and the activation of 'mirror neurons' in

the inferior premotor cortex, inferior frontal gyrus and anterior parietal lobe in the performance and perception of actions (Fadiga et al. 2005; Rizzolatti and Craighero 2004; Rizzolatti et al. 1996).

A number of authors have argued that the peak shift effect is evident in the small Palaeolithic sculptures of human females commonly referred to as 'Venus' figurines, found widely across Europe (e.g. Coss 1968: 280; Spivy 2005: 67–51). Helvenston and Hodgson (2010: 85–86), for example, have recently suggested that they may have been designed as supernormal stimuli with exaggerations to certain aspects of the body, eliciting neurological responses that are greater than normal. This might include 'strong sexual responses' – something that could be tested experimentally by recording the physiological responses (such as pupil dilation) of observers. Some of the figurines appear to be characterised by the gross exaggeration of certain parts of the body, typically the breasts and buttocks, to the point of composing the figures almost entirely, whilst other features (hands, feet, faces, etc.) are played down or disregarded entirely. It is largely the thought that Venus figurines have exaggerated features that has given rise to their universalistic interpretation as the images of a 'mother goddess' and/or their association with fertility (Ehrenberg 1989; see also Russell 1998; Ucko 1968). Other theories proposed for apparent exaggerated distortions range from a preoccupation with pregnancy (Russell 2006) to self-representation (McDermott 1996).

But in many, if not most cases, it is not so much exaggeration but an emphasis placed on certain parts (especially the hips, buttocks, breasts and sometimes abdomen) by the playing down of other features (such as small and narrow shoulders, a lack of arms or feet or atrophied arms or feet). Thigh size, for example, may be emphasised by reducing the size of the lower leg and foot or omitting them entirely. Breasts may appear enormous because shoulders, arms and hands are reduced in size or omitted (Guthrie 2005: 342). There is also great variability in the form of Palaeolithic figurines, and certainly not all display exaggerated features (Nelson 1990). Many may in fact have natural proportions (Ehrenberg 1989) and lack breasts or other sexual features (Hays-Gilpin 2003: 19). The same applies to other types of representation, such as late Upper Palaeolithic engravings on plaquettes as well as parietal engravings and paintings where apparent exaggeration of some features may be the result of the reduction or omission of others (Rosenfeld 1977).

It may therefore be unlikely that the peak shift effect has influenced the nature of Palaeolithic figurines, although it is possible for a limited few cases. In addition to these and figures in rock art that imply vigorous movement, the theory may also apply to the depiction of human form in contorted postures and those that emphasise or accentuate salient curves of the body (Guthrie 2005: 331), such as the low-relief sculptures of reclining women at La Magdelaine (see

e.g. Ucko and Rosenfeld 1967: 210–211). Such depictions may stimulate those neural mechanisms representing 'amorousness' (i.e. high limbic system activation as a result of sign stimuli) (Coss 1965: 15–16; Ramachandran and Hirstein 1999: 18). It must be noted, however, that attempts to explain depictions of females in relation to their sexuality or eroticism (e.g. Guthrie 1984) also risk being criticised as androcentric interpretations (e.g. Delporte 1993; Ehrenberg 1989).

Sexual imagery

In a similar sense to the significance of animals (perceived as potential threats or food sources), sex is obviously another human desire or cognitive preoccupation that has not changed since the Palaeolithic (Bednarik 1986; Calvin 1996: 66; Onians 2000). The concern with sexual activity in palaeoart is important to consider further in terms of the perceptual salience and significance of the human form and its direct relationship with mate selection and innate sexual drives. The depiction of anthropomorphous imagery may directly reflect these primary needs and may be determined by related cognitive tendencies and mechanisms of the emotional brain (Onians 2000; Onians and Collins 1978).

Perhaps surprisingly, depictions of coitus are relatively scarce in the palaeoart of some regions such as south-western Europe (Bahn 1998: 178–179). However, many vivid depictions of sexual activity portrayed in various ways may be found throughout the world, such as those in caves from Siberia to the Iberian Peninsula (Garcia Diez and Angulo 2006); sites in Waterflow, New Mexico; Pilbara region, Western Australia (Wright 1968), and Arnhem Land, northern Australia (Gunn pers. comm. 2008; Hunger 1986; Jelínek 1974; for further examples in rock art throughout the world, see Hays-Gilpin 2003). The appearance of this imagery may also be closely related to human psychology and perception (Bednarik 2002: 63; Jelínek 1974), involving limbic system activation and the role of specialised neural mechanisms with a significant sexual-reproductive role (Solso 2003: 166).

The interpretation of many motifs as representations of female genitalia, particularly ovoid, triangular, and sub-triangular forms, has also led to theories of a preoccupation with sex by palaeoartists (Bahn 1986, 1998; Guthrie 2005). Petroglyph motifs that many researchers have claimed to resemble vulvas occur in many parts of the world and in different periods and cultures, such as those at Pachene (north-east Bolivia); San Javier (Baja, California); Carnarvon Gorge (Queensland) and other parts of Australia (Bahn 1986: 102); and Palaeolithic sites of south-western Europe, such as La Ferrassie, France (Bahn 1998: 174; Jelínek 1989: 501).

There has been much debate over the interpretation of so-called vulva images (e.g. Bahn 1986, 1998; Delporte 1993). It is certainly possible that vulva-shaped signs were multivalent, and they are certainly open

to alternative interpretation. For example, there is a possible relationship between vulva shapes and horse or other animal hoof print motifs in some regions (Hunger 1986; Lorblanchet 1989: 133). What these motifs represented for their creators is simply unknown to us. It is of course problematic and speculative to assign a unitary meaning to vulva-like shapes or any other motif type without more context or ethnographic data (e.g. Clegg 1988; Watson 2010b). (This is not to say that a unitary meaning may not apply to the art of some cultures. For example, the Sumerians adopted a schematised representation of the pubic triangle as the sign for 'woman' or 'female' [Bahrani 2001: 44].)

In contrast to interpretations concerned with meaning, the influence of human perceptual-neurophysiology may contribute to the widespread appearance of vulva forms in palaeoart. Onians (2000) has suggested that female figures and female genitalia comprise one category of palaeoart that, in addition to their relationship with the sexual desires of (predominantly heterosexual) men, closely correspond with visual stimuli that are of focus in human life. The reproduction of aspects of the female body in graphics and relief sculpture can be understood as a consequence of the genetically determined (and environmentally influenced) capacity for the recognition of features essential to survival. In the male heterosexual brain, this capacity is determined by specialised sets of neurons or feature-detectors that are stimulated by visual imagery of this nature, which may result in sexual arousal (Panksepp 1998: 228).

Although we cannot always be certain whether those who produced palaeoart were male or female (Bahn 1986), there are a number of reasons why males may be more likely to be responsible, and why aspects of heterosexual male neurobiology should be especially considered. For example, neural responses to erotic stimuli include a significantly greater activation of the hypothalamus in males than females, which has been positively correlated with sexual arousal (Karama et al. 2002). A range of behavioural studies also report that men have more erotic fantasies and dreams than women, and that these contain more imagery of genitalia (see Guthrie 2005: 327). These factors contribute to the argument that a prevalence of certain motifs such as genitalia and nude figures may be explained as being the result of their production by adolescent boys (Guthrie 2005). If this is indeed the case, it suggests that a significant difference in male and female neurology may determine the nature of some palaeoart imagery.

It might be expected that a majority of imagery would include aspects of female anatomy, yet the diversity of anthropomorphic imagery (in addition to other forms of palaeoart) does not suggest authorship by adolescent males alone. Of course, male bodies also elicit strong neurological responses in addition to various sexual and social messages (Panksepp 1998: 228). The same arguments may thus be applied to prominent

male forms (isolated phallic forms, ithyphallic and megaphallic figures, etc.) that are similarly widespread in palaeoart (e.g. Garcia Diez and Angulo 2006; Guthrie 2005; Le Quellec 2004: 15–32). This is supported by the phylogenetic longevity of signalling behaviour that may indicate the influence of an *innate releasing mechanism* (a neuro-sensory mechanism responsive to a stimulus that causes an instinctive response) for the detection of a threat. Phallic displays by male primates (other than humans) guarding their troop have been compared with similar displays in human tribal societies, including art objects such as wooden ancestor figures that function as guardians in Dayak villages of Kalimantan, Indonesia (Eibl-Eibesfeldt 1975). Male genitalia is also emphasised by artificial means in Papuan and other societies (Ucko 1970). These insights provide possible interpretative avenues for comparable palaeoart graphics and portable objects. Like vulvas, however, they are forms that are possibly multivalent, and assumptions about the meaning(s) of sexual imagery should be treated with caution (Hays-Gilpin 2003: 62).

When included, sexual characteristics are often exaggerated in human representations (Mountford 1965: 99; Vinnicombe 1976) (cf. Fig. 3). As noted, this emphasises sexual dimorphism, and possibly enhances recognition in sexual signalism. Although they do occur, androgynous figures and figurines (displaying both male and female attributes) are comparatively scarce. More frequently, it cannot be clearly discerned whether a figure has a penis or a vagina (Hays-Gilpin 2003: 15–16). However, a majority of anthropomorphs in many regions of the world have no identifying sexual characteristics (Ehrenberg 1989: 68; Hays-Gilpin 2003: 15), and the depiction of primary sexual organs is generally rare. For example, of around 9000 figures in the Brandberg of Namibia, 81 per cent have no distinguishing indications of sex (Lenssen-Erz 1998). In the Drakensberg of South Africa, this is the case for 89 per cent of a sample of 4500 figures (Vinnicombe 1976). In the Eastern Cape, 81.3 per cent of anthropomorphs have no apparent sexual differentiation (Lewis-Williams 1981). A similar case is also apparent in the Gwion Gwion paintings of north-western Australia. This lack of sexual differentiation is generally thought to be deliberate and in some way meaningful (Solomon 1992, 1994), although it may also have been entirely irrelevant to the artists or societies concerned; sexual representations vary greatly throughout the world and may have been important for some groups and not for others (Hays-Gilpin 2003).

Conclusion

This paper has shown how a consideration of neuroscience and perceptual psychology can help to account for the prevalence of human and human-like imagery in palaeoart and some of their common characteristics. Several common characteristics are also better explained by this approach than by theories such

as those based on cultural diffusion or difficulties in depicting the human form. Recent neuroscientific data, including results of brain imaging studies, reveals that the types of representations of the human body that commonly appear in palaeoart correspond closely with inherent neural structures specifically attuned to their analysis and the ways in which perceptual processes operate. The human form has a particularly special role in visual information processing as a result of social interaction and the importance of conspecifics for survival in everyday life and throughout human evolution. Subsequently, the human form is particularly salient, and like other animal forms, is prioritised for attention. Combined, these factors act as a bias in the depiction of human-like forms and the importance they are given, and influence the ways in which they are portrayed.

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Leigh Marymor's bibliographical database of rock art studies

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